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TRANSLOCATION OF ^{14}C-ASSIMILATES IN CANADA THISTLE AND LEAFY SPURGE

by

© ALAN S. MacDONALD

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled 'Translocation of ^{14}C-assimilates in Canada thistle and leafy spurge' submitted by Alan S. MacDonald in partial fulfilment of the requirements for the degree of Master of Science in Weed Science.

.....
(Supervisor)

.....

.....

DATE.....May 24.....1977

O let me grow
and push
upright!
and ever aware of height
and the cry
to reach a dazzled strangeness
sun-pierced sky.

- Dorothy Livesay

ABSTRACT

Greenhouse and field studies were concerned with the translocation of ^{14}C-assimilates in Canada thistle (*Cirsium arvense* (L.) Scop.) and leafy spurge (*Euphorbia esula* L.). The pattern of distribution of ^{14}C-assimilates was the same for both species. When individual shoots were supplied with $^{14}CO_2$, most of the fixed carbon was retained in the treated shoot but some ^{14}C was exported to the other parts of the plant. The principal sink was the root system.

Translocation of ^{14}C to the roots was rapid; it was faster for Canada thistle than for leafy spurge but the distribution over time was the same. It was not until thistles were 30 days and leafy spurge plants 60 days old that the shoots sent significantly more ^{14}C-assimilates to the rapidly growing areas of the root system than they did at early stages of shoot growth.

In Canada thistle, the export of assimilates to the roots was greater from a mature leaf occupying a middle position on the shoot than from leaves situated either above or below that portion. There was no evidence to support the hypothesis that lower leaves tend to supply the roots with assimilates. The translocation and subsequent distribution within the plant was highly sensitive to temperature. Less ^{14}C was retained in the shoot of plants treated at 10°C than in plants which had received treatment at either 20 or 27°C. Again the principal sink was the root system.

The translocation of assimilates from a primary shoot to a number of secondary shoots present on the root was studied for both species. Of the ^{14}C not retained in the treated shoot, most was found in the

roots and the remainder in the secondary shoots. All secondary shoots received some ^{14}C from the treated primary shoot. The ^{14}C was distributed evenly among the secondary shoots.

The transfer of ^{14}C-assimilates between a secondary shoot or shoots and the primary shoot was examined in Canada thistle plants. Quantitative data are presented and it is concluded that the existence of a reciprocal exchange of assimilates between shoots means that each must simultaneously be both a source and a sink. Shoots and portions of the roots closest to the treated shoot contained slightly more ^{14}C than those more distal. Root buds were noted as major sinks.

In the field, rosettes of Canada thistles were able to export assimilates to a limited extent after exposure to $^{14}CO_2$. The sink areas were the roots, regrowth shoots and other rosettes to which the fed rosette was connected. In the greenhouse, the presence of secondary shoots did not alter the distribution of ^{14}C-assimilates to the roots.

Sectioned material and cleared whole tissues indicate that the connections between the vascular systems of the shoot and the root for Canada thistle and leafy spurge are in many respects similar. The anatomical feature which appears to be significant with respect to the junction is the uninterrupted extension of two collateral bundles from the root stele to the shoot. There is no real evidence of an anatomical block at the site of the junction although accumulation and metabolism of ^{14}C-assimilates in the area of procambial cells could prevent the movement of assimilates or herbicides to a shoot. The procambial cells constitute a "constriction" to assimilate flow rather than an actual block.

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LIST OF ABBREVIATIONS

Co	:	cortex
Pc	:	procambium
Ph	:	phloem
PP	:	perforation plate
R	:	root
RS	:	root stele
S	:	shoot
St	:	starch
V	:	vasculature
VB	:	vascular bundle
VM	:	vessel member

INTRODUCTION

In the control of perennial weeds, there are two main objectives: the prevention of seeding and the eradication of already established plants. Seed production is an important factor in the spread from one location to another. Within a localized area, however, the continued growth and extension of vegetative propagules may be more important than seed production (21, 27, 29, 30, 31, 46). Creeping perennials such as Canada thistle (*Cirsium arvense* (L.) Scop.) and leafy spurge (*Euphorbia esula* L.) have root systems extending several feet below the cultivated zone and regenerate from these depths by means of buds, originating on the roots (3, 27). The use of foliar-applied systemic herbicides has made it possible to kill underground portions of plants and, therefore, offers particular advantages against established weeds.

Although a herbicide may be translocated to portions of the root, complete control is rarely achieved. The effectiveness of any herbicide is dependent upon the amount of chemical that reaches a site of phytotoxic action within the plant. In perennial weeds, if insufficient herbicide accumulates in portions of the plant, for example the roots, then rapid recovery is possible. New shoots capable of seed-set and vegetative reproduction result. The potential source of infestation remains, making control measures seemingly counterproductive.

Gottrup (23), in an examination of the translocation of the herbicide, glyphosate, in creeping perennial weeds, found that

^{14}C-glyphosate and ^{14}C-assimilates were not distributed to all parts of the plant after the treatment of individual shoots. The majority of recovered radioactivity remained in the treated area, a small amount was recovered from the roots, and labelled material was recovered from some "secondary" shoots while absent in others. The phenomenon, which the author terms "bypass", remains unexplained, but field and greenhouse studies of glyphosate translocation in quackgrass rhizomes (*Agropyron repens* L. Beauv.) indicate a similar situation (8, 59, 60).

It is generally held that foliarly applied phloem-mobile herbicides move together with assimilates in plants (53). Based on this assumption, knowledge of assimilate translocation has been useful in the prediction of translocation patterns for such herbicides. The translocation of labelled assimilates has been examined extensively already for a number of perennial weedy grasses (9, 17, 19, 22, 32, 40, 47, 48, 54). The present study involves the translocation of assimilates in two dicotyledonous perennials: Canada thistle and leafy spurge.

Why some secondary shoots should import herbicide or assimilates and not others remains speculative, but it is probably the result of one or more processes. The growth stage of both primary and secondary shoots influences whether a shoot has an importing or exporting role with respect to photosynthates and herbicide. In addition, the metabolic activity and demands of various meristems influence the relative distribution of both. Finally, the possibility of an anatomical constriction, partial or complete, exists. Crushing of various cells and incomplete differentiation leading to an acute constriction has been reported to take place in the leaf base of

Lolium perenne L. (18).

Few references in the literature deal specifically with the root anatomy of Canada thistle and leafy spurge; reports to date have been mainly concerned with an account of morphology (3, 25, 27, 51), descriptions of root buds and distribution (10, 11, 45) and regenerative capacity of roots (26, 52). Shoots of leafy spurge originating on the hypocotyl have been described in terms of distribution of buds (49) and the inception of vascular connections (50). However, no anatomical information describing the vasculature of emerged shoots present on the roots is available for either Canada thistle or leafy spurge. An examination of the root-shoot junction is necessary to determine whether there is in fact any basis for an anatomical barrier to transport.

To successfully control Canada thistle and leafy spurge, it is important to gain an understanding of the physiological events taking place within the whole plant, obtained in part from assimilate translocation studies. In addition, it is necessary to clarify the anatomical nature of vascular connections in the plant. The significance of the translocation system design, particularly the vascular corridor between the stele of the parent root and the vascular bundles of the daughter shoots, becomes evident for the interpretation of nutrition to new shoots and the understanding of herbicide and assimilate movement.

LITERATURE REVIEW

Glyphosate, a non-selective postemergent herbicide, has been used with a certain degree of success in the control of perennial weed species (59, 60, 61). Once applied to the foliage, the herbicide can be translocated to the underground portions of perennials and exert its lethal effect (2, 55). Although Canada thistle is susceptible to glyphosate, leafy spurge is resistant (61). The interception of spray and greater absorption by the leaves of Canada thistle have been suggested as possible reasons for the differences in susceptibility (24).

Gottrup (23) was able to demonstrate that glyphosate gave good control of Canada thistle when the herbicide was translocated via the root, to the shoots other than the one treated. If one of a number of shoots present on the same root section was sprayed with glyphosate, injury symptoms usually appeared in all of the shoots. This was true regardless of whether the end-shoot treated was larger or smaller than the remaining shoots. There were isolated instances, however, where secondary shoots lacked injury symptoms. These shoots, according to the author, were "by-passed" by the herbicide. Subsequent experiments involving the use of ^{14}C-glyphosate gave further evidence of by-pass in secondary shoots. The distribution of ^{14}C-glyphosate-treated plants of both Canada thistle and leafy spurge was confined to the treated shoot, although some labelled material was detected in the roots and the secondary shoots. Such shoots, however, were sometimes lacking in ^{14}C-glyphosate. Preliminary experiments in ^{14}C-assimilate translocation in the field with plants of Canada thistle, leafy spurge and

toadflax gave similar observations. In these cases, labelled assimilates sometimes only went to portions of the root and developing buds.

Experiences much like the "by-pass" phenomenon described by Gottrup (23) have been reported for other weeds. Glyphosate has been effective in quack grass control (59, 60) and foliage sprays drastically reduce bud survival (8). In some instances after glyphosate application in the field, healthy rhizome sections could be found between dead sections on either side (60). Treatment of individual shoots in the greenhouse resulted in similar observations (59). Claus and Behrens (8) observed that not all rhizomes were killed following glyphosate application; rhizomes closest to the mother shoot survived and greater bud kill took place at the rhizome tip, that portion most distant from the treated mother plant. The radioactivity recovered from rhizome segments after the application of ^{14}C-glyphosate to the treated mother shoot indicated that, even though radioactivity was present in all rhizome segments, the greatest amount was recovered from rhizome tips and the least from the segments near the treated parent plant. Increased bud kill near the rhizome tip was attributed to preferential glyphosate accumulation (8).

Forde (18) refers to an unpublished study in which he found that when $^{14}CO_2$ was administered to an immature leaf of *Lolium perenne* L., little or notradioactivity moved through the intercalary meristem into the remainder of the plant. When a mature leaf was so fed, however, considerable activity passed to other parts of the same plant, presumably translocated via the leaf base. Since trace amounts of radioactivity were detected beyond the treated leaf in the case of the

immature leaf, the leaf base represents a restriction to assimilate translocation rather than an absolute barrier. Sectioned material of the base of the young leaf revealed an anatomical constriction; sometimes complete blockage of the phloem can occur over short distances (18). Such a barrier resulted from a "delay in basipetal differentiation and early crushing of the first formed phloem elements" by the expansion of the surrounding cells. A mature leaf showed no such constriction at the base. Thus, the observed restriction on the translocation of assimilates was to a large extent anatomical rather than metabolic.

Translocation of Assimilates

The mechanisms and general pattern of assimilate translocation have been extensively reviewed (37, 42). It is generally agreed that assimilates move from areas of synthesis (sources) to areas of consumption (sinks). Assimilates move between sources and sinks to meet demands throughout the plant; growing organs develop at the expense of either current photosynthate or stored reserves. The pattern of distribution is not rigid and the areas of supply (leaves) and points of demand (developing organs) change during the course of development, particularly during reproductive phases and when the plant is either partially or completely defoliated. By introducing a leaf or whole plant to a $^{14}CO_2$-containing atmosphere, it is possible by autoradiographs or quantitative determinations of radioactivity to determine the distribution pattern of assimilates.

Little reference is made in the literature to the assimilate distribution patterns in perennial dicotyledonous weed species using ^{14}C as a tracer. Available reports to date have been restricted to a discussion of *Sonchus arvenis* L. (20) and two species of *Oxalis* (7). During early growth, a leaf requires carbohydrate for its development and will show a net import of assimilates until it reaches a certain size and export begins. In *Sonchus*, a young leaf 3 cm long was able to translocate assimilates (20). The aerial shoots of *O. latifolia* and *O. pes-capre* reached a stage of five and eight leaves, respectively, before they were no longer dependent on the large root reserve of carbohydrate stored in the parent bulb (7). Up until this stage, there was a lack of import to the roots, although initial root development

was supported by the parent bulb. As a leaf reached a stage where export of assimilates was possible, the assimilates were directed towards the apex. When one leaf of a rosette is exposed to $^{14}CO_2$, it has been shown that, in *Sonchus*, the labelled assimilates are directed towards the apices of the other rosette leaves and to roots provided these roots are actively growing (20). There is a stage from five or eight leaves to twenty-five or thirty-two leaves in *O. latifolia* and *O. pes-capre*, respectively, at which substantial amounts of labelled assimilates move out of aerial parts. The sinks in these instances are the tubers and new bulbils. As a plant continues to grow, the particular leaf mentioned becomes more spatially separated from the apex but export continues. In *Sonchus*, treatment of a leaf at this stage is marked by a decline in export of assimilates to other leaves of the rosette and a corresponding increase in assimilates directed towards the developing roots. In *Oxalis*, progressively smaller amounts of labelled assimilates move into the distal parts of the tubers, although the now well-developed new bulbils assume increased prominence as sinks, reflected in the substantial amounts of ^{14}C accumulated there.

With the onset of reproduction, changes in the pattern of assimilate distribution take place. Developing fruits show an overwhelming demand for assimilates. Results of exposure of *Sonchus* to $^{14}CO_2$ at this stage indicate that the highest concentration of ^{14}C apart from the treated shoot was found in branches, leaves and flower buds of the stem. The acropetally directed assimilate transport is most intense at this stage. Roots function with difficulty because their demands for photosynthate are overshadowed by the requirement of

the fruit. After the flowering stage and when the aerial parts senesce, the largest amount of radioactivity was directed to the roots. In *Oxalis*, as the aerial shoots become senescent and less efficient in fixing $^{14}CO_2$ and exporting assimilates, the bulbils still receive some of the assimilates. The bulbils, in addition, have some of the substrate requirements for further development provided by reserves present in the tubers.

The general pattern of assimilate translocation remains the same even if the system examined is altered to include secondary shoots. In *Sonchus*, for example, shoots can develop along the same root secions, and are not dependent upon one another in assimilate supply (20). When one of a series of shoots is exposed to an atmosphere containing $^{14}CO_2$, the translocation to the additional shoots is very limited. Of the total recovered radioactivity, the additional shoots had a lower proportion than the parent root from which they are derived. The highest concentration of ^{14}C, apart from the treated shoot, was found in the rapidly growing roots found on the mother root. When one shoot is present on the root stock, and that shoot is exposed to $^{14}CO_2$, the labelled assimilates can be found in the root within minutes. In instances where more than one shoot is present on the same root stock, little radioactivity is recovered beyond the treated area even if the period after initial assimilation is several days.

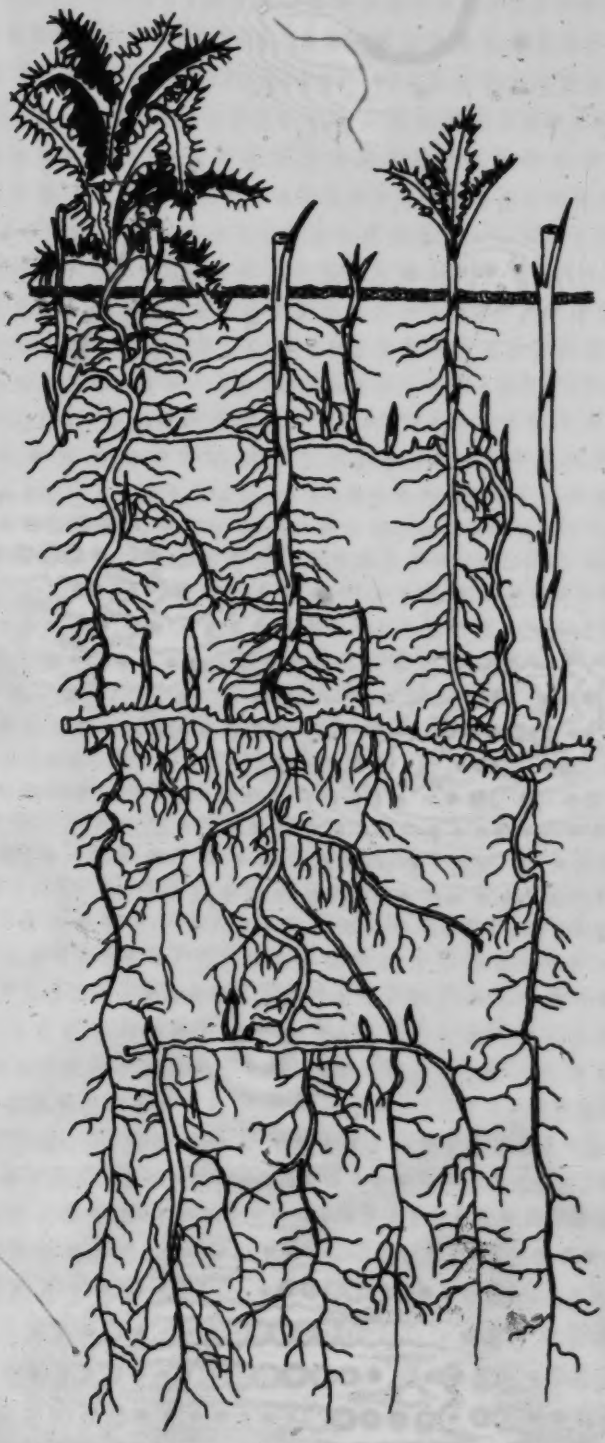
The pattern of assimilate distribution in perennial weedy grasses with rhizomes and/or rhizome tillers (17, 19, 32, 47, 48, 54) and in non-rhizomatous species (9, 40, 63) is comparable to that described for dicotyledonous species. During seedling growth, assimilates are distributed to the shoot tip, the developing leaves of the primary

shoot, and to the roots. With the outgrowth of buds, the assimilates are diverted to the developing rhizomes and tillers. Tillers in *Lolium multiflorum* Lam. (9, 40) and *Poa pratense* L. (47, 48) and rhizomes in other grasses (17, 19, 32) demonstrate a reciprocal transfer of assimilates to the parent primary shoot. A somewhat different pattern was reported more recently in *Agropyron repens* L. Beauv. by Rogan and Smith (54) who did not find a reciprocal exchange in assimilates between the main shoot and tillers. The pattern in the mature plant with a well established and integrated system of primary and secondary rhizomes and tillers is one of increasing independence of individual shoots and declining support from the parent to the daughter. In other words, assimilates initially move to the daughter tillers or rhizomes which act as sinks, but with increasing age and independence of the secondary shoot system, these shoots later act as sources of assimilate supply. Parent shoots then are able to direct assimilates to the roots. When parts of the whole plant are defoliated, labelled assimilates move from the independent tillers to parts of the plant subject to the stress. Such an occurrence has been observed in both non-rhizomatous grasses (22, 33, 35) and in rhizomatous species (17, 19, 32, 47, 48, 54). The stress conditions result in a reversal of the normal direction and patterns of translocation. In perennial grasses, at least, the absolute independence of secondary shoots remains controversial.

Canada Thistle

Canada thistle, probably native to Southeastern Europe and the eastern Mediterranean area (43, 44) is a serious weed of agricultural lands of all types and is one of the most troublesome weeds of temperate regions (1, 4, 6, 21, 27, 29, 30, 31, 34, 56). It is the only thistle with separate male and female plants (43). Although seeds may be important in spreading the species to new and more distant areas, successful germination quite often depends on a large number of factors (36). The key plant organ responsible for local infestation is the root (6, 26, 27, 30, 56). Established seedlings develop a tap-fibrous root but quickly produce a number of laterals which extend 6 to 12 cm before either descending in a vertical direction or continuing to spread laterally (43). The subterranean system of Canada thistle, illustrated in Figure 1, is comprised of both root and shoot structures, however (27, 35, 43, 56). Adventitious buds are produced both on the original vertically descending roots and the numerous lateral roots. Buds originating on the latter appear as the root system spreads. Such buds produce leafy shoots once they reach the soil surface. The ability of lateral roots to develop shoots is greatest in spring and least in summer (34). The mature seedling is termed the primary shoot and the other shoots which develop from the roots subsequently are, therefore, secondary shoots. The root system has, in addition, been further broken down into three categories. The first category is the spindle-like primary root or thickened main root of the seedling; it descends vertically. The broadened root structure is the result of accumulation of food reserves from the developing seedling (27). The second category

FIGURE 1. The underground root system of Canada thistle. Redrawn from Weeds of California, p. 451. (Weeds of California by W.W. Robbins, M.K. Bellue, and W.S. Ball, California State Department of Agriculture, Sacramento, 544 pp.)



includes the horizontally directed roots which bend either upward or downward before branching into a number of vertical roots. This particular type has also been termed "root runners" (35) because of the extensive creeping nature. The majority of new shoots which originate from the roots develop from this type. Finally, the third category includes the numerous short adventitious roots which function in absorption and nutrient uptake. Such roots are more numerous on the vertical roots than on the horizontal ones (27).

The ability of the root to regenerate from small fragments has already been demonstrated (26). Usually the number of shoots per unit length of root was greater if the root was fragmented into many short pieces rather than a few long ones. The presence or absence of visible buds on the root does not influence the ability to produce new shoots. Root fragments less than 5 mm long are unable to generate a new plant (26).

The characteristic features of Canada thistle root anatomy have been described (25, 35, 56). The xylem arrangement of the root is diarch with the two main parenchyma rays and a number of narrower rays. The stele of the root consists mostly of thick-walled fibres with secondary vessel members scattered but usually arranged in a few radiating rows and phloem forming a fan-shaped area on the periphery. Although the stele forms a well developed woody cylinder, secondary growth is limited; neither cortex nor epidermis are shed to any extent. The cortex consists of many layers of more or less circular parenchyma cells and is also well developed. These basic characteristics are common to all of the root categories described earlier. Adventitious buds are scattered on the roots, and have an endogenous origin from

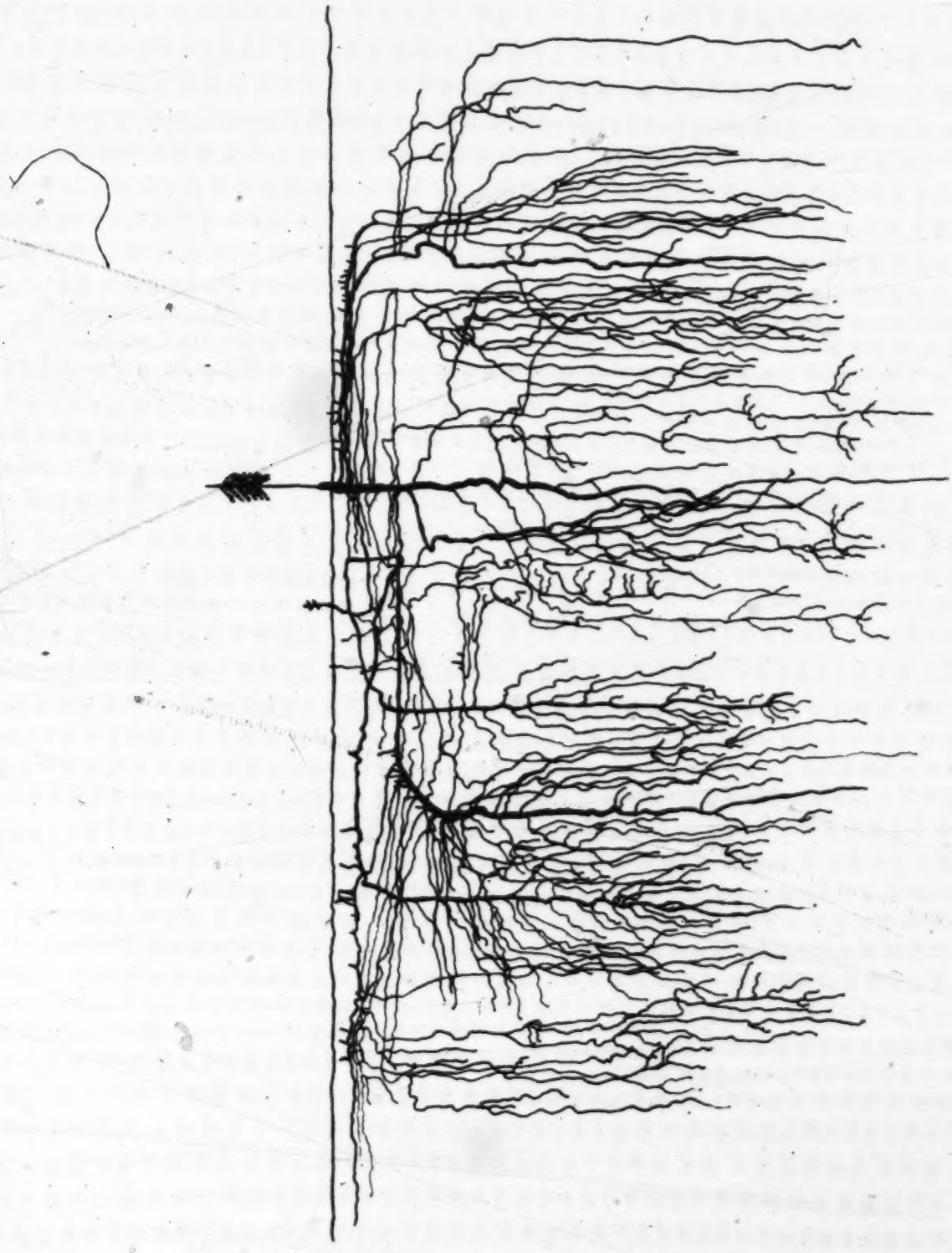
pericyclic tissue. The shoot buds and root initials originate near the protoxylem poles of the root and establish continuity with the vascular system of the primordia.

Leafy Spurge

Leafy spurge is a tenacious weed introduced from Europe and is particularly well established in Western Canada and other parts of North America (57). The seriousness of this species as a weed is attributed to its capacity to persist under adverse conditions and to its mode of reproduction (3, 5). The root plays a role in both these characteristics. The underground portions of leafy spurge are outlined in Figure 2. The longitudinal extension of the primary root is described in terms of horizontal and vertical "long" roots (51). They are not considered different morphological entities but, rather, they represent different aspects of the same root. Before the initiation of cambial activity, long roots are able to produce a number of lateral projections termed "short" roots. Such roots are characterized by limited growth, absence of secondary growth, and the inability to produce buds. In addition, lateral long roots can be formed, but their presence is delayed until after cambial activity takes place. Some of the smallest of "long" roots, particularly at a young stage, resemble at least superficially the "short" roots. The two categories remain distinct because only the long roots are able to produce new shoots from buds.

In intensive investigations, concentrated primarily in Saskatchewan, Canada, the great regenerative potential of leafy spurge was evident from the large numbers of buds found on the root and the depths from which they emerged. The roots of leafy spurge penetrate to a depth of 2.8 m but the greatest proportion of the total weight was found in the upper 15 cm of the soil (10). The majority of the buds giving rise to new shoots are found in the top 30 cm of the soil (11, 12). Leafy

FIGURE 2. The underground root system of leafy spurge. Redrawn from Hayden (27).



spurge shoots emerged from roots located 0.9 m below the soil surface after the upper soil had been removed and replaced by well tramped fresh soil (12). Although the frequency of shoot buds decreased with increased depth of soil, it has been demonstrated that roots at the greatest depths do not differ in regenerative capacity from those found in the upper layers of the soil (52). Even though the regenerative capacity is lowest in June, and highest at flowering, root fragments have the ability to produce new shoots even in the absence of preformed buds.

Anatomical studies carried out on roots have indicated that all underground structures were in fact roots (45). Previous reports in the literature indicated the presence of both roots and rhizomes (10, 11, 12, 57), although Raju (51) indicated that his "long" roots were the rhizomes of earlier reports. The anatomy of leafy spurge resembles closely that described for *Euphorbia cyperiass* L. (35). The xylem arrangement is mainly triarch although tetrarch and polyarch (5, 51) arrangements have been reported. The "short" roots designated by Raju (51) do not undergo secondary growth and are diarch at the ends, but the remainder of the root is triarch (45). Usually secondary growth is prolific in roots, resulting in a strongly developed central stele. Unlike Canada thistle, secondary growth is not restricted. The cylindrical woody core can occupy as much as two thirds of the total tissue (5). The vessel members are few in number and the bulk of the secondary growth is comprised of thick walled tracheids. Quite often a single row of cells separates the xylem arms. The vessel members are found in rows radiating from the center.

MATERIALS AND METHODS

Experiments were conducted in the greenhouse during 1974-1976, and in the field during 1975 and 1976.

Plant Material

Plants used were Canada thistle (*Cirsium arvense* (L.) Scop.) and leafy spurge (*Euphorbia esula* L.) started from seed. A single plant from each species became the stock plant for all the experiments. Both Canada thistle and leafy spurge were propagated vegetatively from root pieces of the stock plants to avoid genetic variability. In the case of leafy spurge, only roots of the "long-root" type described by Raju (52) were used. Canada thistle roots were chosen without such selection. Each of the root pieces, once cut, had all the adventitious roots removed. In early experiments, root pieces 5 cm in length were placed in 8 x 8 x 5 cm plastic cups with 3:2:1 soil mix (Malmo clay loam:peat: sand) and later were transplanted to 15 cm pots. Pieces 15 or 30 cm in length were planted in plastic trays measuring 30 x 30 x 5 cm. Later, to promote initial root growth, the starting medium for all root pieces was changed to (horticultural) vermiculite. Young plants then were transferred to soil after 4 or 5 weeks. During this period, the plants were supplied every third day with nutrients in the form of Hoagland's solution No. 1 (28). Tap water was supplied as required. Plants were maintained in growth chambers and under greenhouse conditions set to provide a 16 hour photoperiod. At plant level, the light intensity was between 14 and 16 klux from a suspended bank of

fluorescent and incandescent lamps. Relative humidity was 40-50%, although lower values sometimes were recorded in the greenhouse. A constant temperature of 20 ± 2°C was maintained throughout the experimental period unless otherwise specified. Some seasonal temperature fluctuations were experienced in the greenhouse.

For field studies, 10-day-old emerged shoots from greenhouse material were transplanted to Malmo clay loam field plots. Plants grown from 5 cm pieces were placed at 0.5 m intervals while those grown from 15 cm pieces were placed at intervals of 1.0 m. The production of secondary shoots was greater from the longer root pieces. The plots were kept weed-free during the growing season.

For anatomical investigations, Canada thistle and leafy spurge were grown from 5-cm pieces of root. Plants with emerged shoots after 14 to 20 days were trimmed with a razor blade to include the base of the shoot and the junction of the root and shoot. Although the Canada thistle roots ranged in diameter from 2 to 4 mm, the material was otherwise uniform.

Application of $^{14}CO_2$ Treatments

Unless otherwise specified, the description of treatment offered applies to all experiments. In all cases, labelled carbon was introduced to the plant and assimilation was allowed to take place in an atmosphere containing $^{14}CO_2$. The plant or plant part to be exposed was enclosed in a transparent vessel and sealed with a silicone lubricant (Dow Corning Brand). The assimilation chamber was a 38 x 38 x 76 cm plexiglass box, a belljar with diameter 25 cm, or a glass cylinder 34 cm high and 9 cm in diameter. The carbon dioxide was

generated from outside the chamber and the atmosphere was stirred by a battery-operated fan in the case of the box, or by an air pump (Neptune Dyna pump) in the case of the glass vessels. The assimilation treatments were carried out between 8:00 and 10:00 a.m. in the greenhouse where daylight was supplemented by artificial lighting from fluorescent and incandescent lamps. After the assimilation period, which was 10 minutes or 1 hour, the chamber was flushed with a vacuum pump and then removed from the plants. Treated plants remained in the greenhouse until they were harvested. The time between the assimilation period and killing of the plant varied, depending on the nature of the experiment, but usually translocation was allowed to take place for 24 hours.

The procedure adopted for the generation of $^{14}CO_2$ atmosphere was as follows: 2 mg of $Ba^{14}CO_2$ (specific activity 5 mCi/mole) containing 50 μCi was preweighed into a vial. The addition of 2 ml of lactic acid liberated the $^{14}CO_2$. Two Erlenmeyer flasks, each containing 250 ml of 1N NaOH, were connected in series to a vacuum pump to trap any unfixed $^{14}CO_2$ not utilized in the assimilation chamber.

Experimental Design

All experiments were designed as randomized complete blocks. Some difficulty was encountered in selecting uniform plant material for replicates, and selection sometimes was made on the basis of leaf stage, leaf length, or plant height. All treatments were replicated at least three times; each replicate consisted of one plant. In some experiments five or six plants were given the same treatment; some of these plants were assayed by autoradiographic methods and some were

assayed for radioactivity by extraction and counting.

Quantitative Determinations

After harvesting and washing, samples were divided into component parts and fresh weights were determined. The plant material was ground immediately in ethanol (95%) in a Sorvall mixer for five minutes, or it was stored in a freezer at -20°C until extraction was possible. The ground homogenate was filtered quantitatively through Whatman No.1 filter paper in a Buchner funnel, and aliquots of 1 ml of the filtrate were combined with 15 ml of liquid scintillation fluid for counting in initial experiments. Plant residues and ethanol-insoluble components were also assayed for radioactivity by drying at 50°C, grinding in a Wiley mill, and placing 20 mg aliquots in 15 ml of Aquasol (Nuclear Chicago) to determine the amount of radioactivity in each sample. The amount of ^{14}C in the plant residue was negligible; counts were only slightly above background in all samples tested, so the procedure was discontinued in future experiments. An accurate assessment of total activity recovered was possible with ethanol extraction of fresh material.

All quantitative determinations of radioactivity were done on a LS-200B Beckman Liquid scintillation spectrometer. Samples were counted for 10 minutes or until counting error was 0.5 %. The scintillation fluid was prepared by dissolving 120 g of naphthalene, 6 g 2,5-diphenyloxazol (PPO) and 0.5 g 1,4-*bis*-2-(5-phenyloxazolyl)-benzene (POPOP) in p-dioxane to make up one liter. Samples of 1 ml were counted in this at room temperature after a period of dark adaptation. Counting efficiency was determined by a channels ratio method

(62). Channels ratio was plotted against efficiency (Figure 3) to obtain a quench correction curve. If chemically quenched standards are used to construct an efficiency curve and such a curve is applied to correct for efficiency of coloured samples, then the channels ratio method gives acceptable precision (14). Using the efficiency value obtained, activity in counts per minute in each sample then was converted to disintegrations per minute.

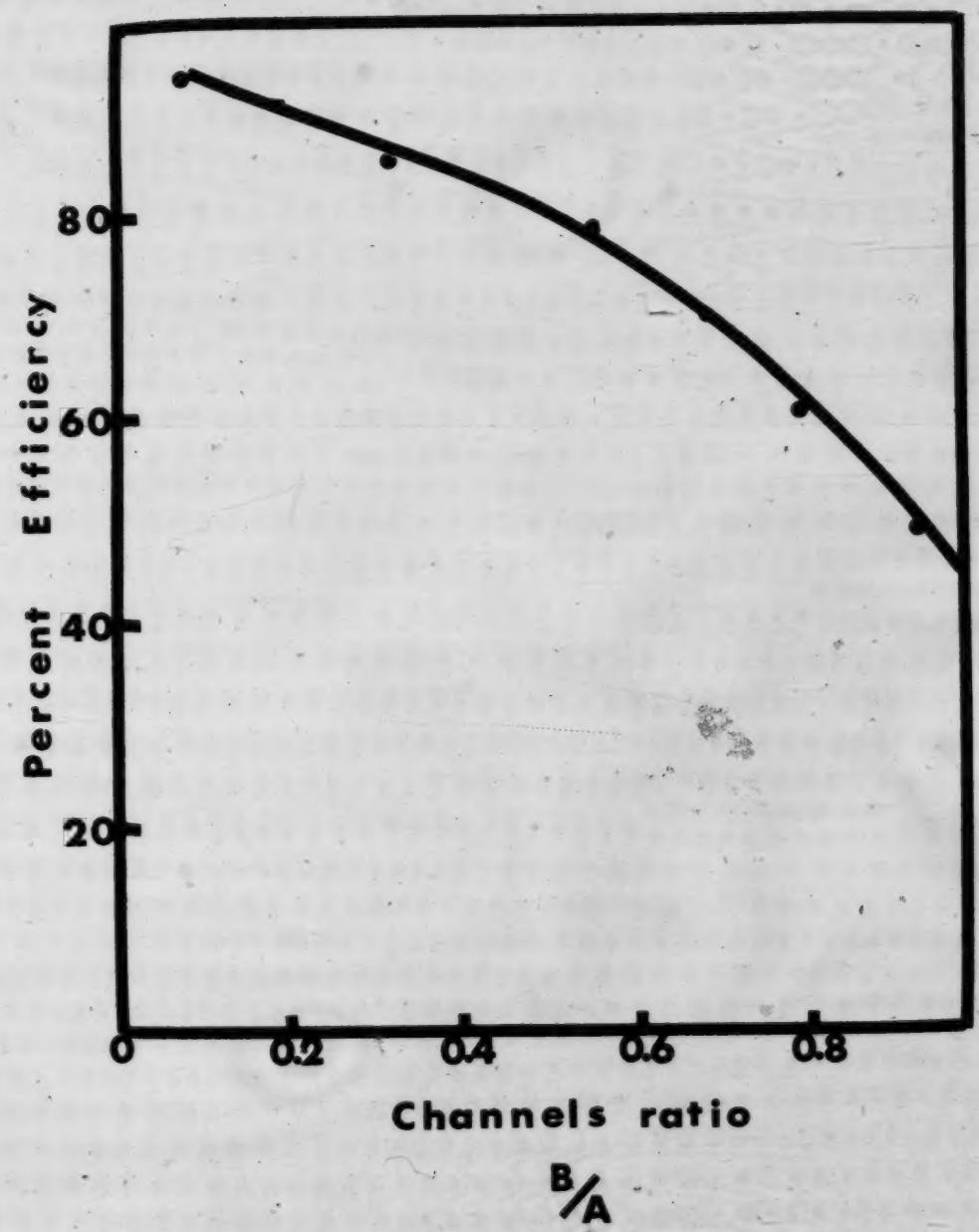
Autoradiographic Assay

The preparation of autoradiograms was carried out according to the procedure described by Crafts and Yamaguchi (13). Harvested plants were placed intact on cardboard, freeze-killed, and placed in a freeze drier for 90 hours. Field material was mounted after excavation from the soil, frozen with crushed dry ice, and then brought to the laboratory. Freeze-dried material was humidified for 12 hours, compressed, and remounted on cardboard (10" x 12") before exposure to Kodak Blue Brand Medical X-ray film for 24 hours to one week. Films were developed at 21°C for 2 minutes and fixed for 10 minutes in Kodak fixer. To check for artifacts, untreated plants were handled in the same manner.

Microtechnique

Material prepared for paraffin sectioning was fixed in formalin: acetic acid:alcohol, 18:1:1 v/v (ethyl alcohol 50%, glacial acetic acid, commercial formalin [37% formaldehyde]) for 12 hours and was then washed in water for 12 hours. Tissues were then dehydrated in a TBA series (Johansen, 1940) as described by Jensen (33). This consists

FIGURE 3. Quench correction curve used for ^{14}C assay in LS-200B Beckman liquid scintillation spectrometer. Counting efficiency was determined by a Channels ratio method.


Percent Efficiency
80
60
40
20
0
0.2
0.4
0.6
0.8
Channels ratio
B/A

of mixtures of tertiary butyl alcohol (TBA), ethyl alcohol, and water; the ethyl alcohol and water being replaced by TBA in the higher members of the series. Infiltration and embedding in "Paraplast-Plus" (M.P. 56°-57°C) followed dehydration. Blocks were sectioned at 10-15 µm on a rotary microtome (Leitz Wetzlar). Paraffin ribbons were fixed on glass slides with Haupt's adhesive (33). Sectioned material was stained with safranin and counterstained with fast green (MCB). Some sections were stained with Schiff's reagent by following the PAS (Periodic acid Schiff's) method (33) to determine the distribution of starch. Both staining procedures provided adequate specimen contrast.

For anatomical study, the clearing of root-shoot junctions was accomplished by boiling the tissue in water and 2:1 95% ethanol and acetic acid before transferring to 10% NaOH for 12 hours or until discoloration was complete. Dehydration in successive grades of alcohol and xylene to 100% xylene promoted optimal clearing. After several days in xylene, the material was dehydrated again and stored in methyl salicylate.

Photography

Observations of sectioned material were made with a Zeiss photomicroscope; bright field optics were routinely used. The cleared whole tissue was examined with transmitted light at X10 magnification. All photographs for light microscopy were taken on Panatomic-X black and white film and all others were taken on Kodak Plus-X Pan black and white film. All films were processed in Kodak developer D-19 (1:1 dilution) at 20°C.

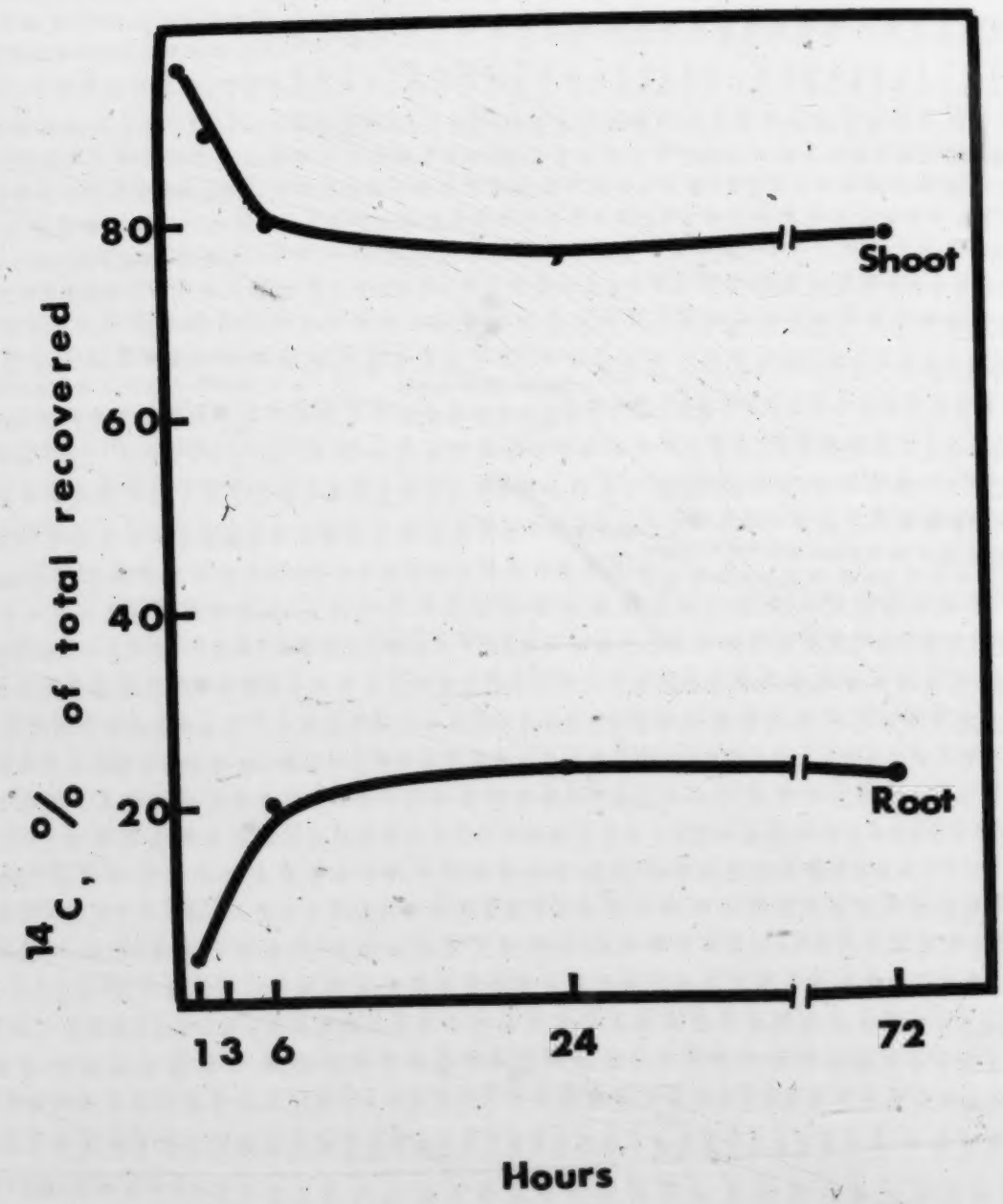
RESULTS

Translocation of ^{14}C-assimilates in Canada thistle

A preliminary experiment was carried out in the greenhouse to determine the changes in distribution of labelled assimilates over time in both roots and shoots of thistle. The purpose of the experiment was to determine the optimal time for harvesting $^{14}CO_2$-exposed plants, such that the greatest amount of ^{14}C was translocated from fed whole shoots to other portions of the plant. In addition, the experiment was carried out to determine when the plant should be harvested to give sufficient ^{14}C that the amount recovered could be determined with a high degree of certainty. Single plants 7 weeks old were exposed to $^{14}CO_2$ for 10 minutes and harvested after 1, 3, 6, 24 and 72 hours. Each of the five treatments was replicated three times. Plants were separated into shoots and roots and the ^{14}C present in each was expressed as a percent of the total recovered from each plant (Figure 4).

The amount of radioactivity recovered from $^{14}CO_2$-exposed plants after one hour was approximately 4,300,000 dpm per plant whereas after 72 hours the amount was 1,900,000 dpm per plant. The decrease in activity in the plant indicates a loss of ^{14}C. This decline was thought to be due to one of two reasons. Firstly, the ^{14}C may be present in a form which is insoluble in the ethanol medium. The possibility of the ^{14}C being incorporated into ethanol-insoluble plant parts exists. To test this hypothesis, samples of the extracted plant residues were counted in a liquid scintillation counter. The total activity detected in such samples was slightly above background level. No increase in incorporation was

FIGURE 4. Time course of the distribution of ^{14}C in the shoots and roots of 7-week-old Canada thistle plants after exposure to $^{14}CO_2$.


80
60
40
20
^{14}C, % of total recovered
Shoot
Root
1 3 6
24
72
Hours

detected over the 72 hour period. Secondly, some of the ^{14}C could be lost to the environment. The decrease in recovered ^{14}C was attributed, therefore, to respiratory losses as $^{14}CO_2$.

As shown in Figure 4 not much radioactivity had accumulated in the roots after one hour; at most 4.0% (i.e. approximately 42,000 dpm) was recovered from the roots. Radioactivity accumulated rapidly, however, within the first three to six hours after treatment, and then decreased slightly. The percentage of total activity in the roots increased until 24 hours after exposure, reaching a maximum of 23%, but it did not increase further during the remainder of the test period. The percentage recovered from each plant part continued to decline after 24 hours. These observations indicate that the distribution of assimilates consists of an initial phase of rapid translocation to the roots followed by a lag phase during which the amount of assimilates stays at an equilibrium. The bulk of the ^{14}C-assimilates, nevertheless, remains in the fed shoot; only 23% was translocated after 24 hours. Harvesting of plants after 24 hours allows the maximum amount of ^{14}C assimilates to be translocated from a fed shoot.

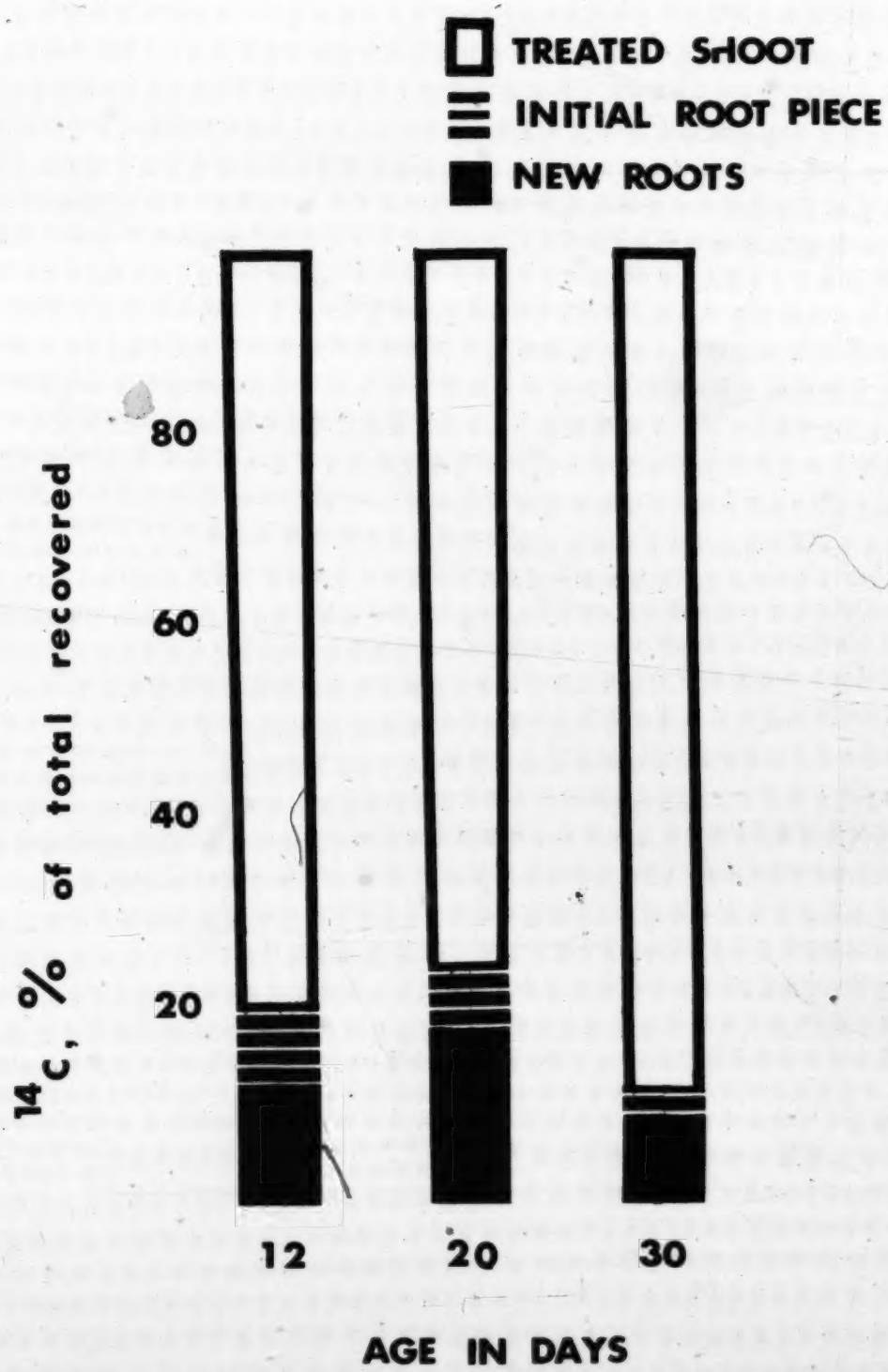
Although all plants were of approximately the same size and leaf area, there was some variability in total $^{14}CO_2$ fixed by the plants. However, there was close agreement between replicates in all the treatments of this experiment.

Thistle shoots grown from root pieces initially depend on stored root reserves for energy supply but gradually reach a stage where they are able to export assimilates to the roots. In order to determine at what growth stage young rosettes are able to transport assimilates to the roots, thistles 12, 20 and 30 days old, grown from 5-cm root pieces,

were exposed to $^{14}CO_2$ and the radioactivity present in each plant was determined after 24 hours. The length of the largest fully expanded leaf at each growth stage was 3 cm, 5 cm and 15 cm, respectively. At the time of harvest, plants were separated into (1) treated shoot, (2) initial 5-cm root piece and (3) new roots which grew from the starter root piece. Each treatment was replicated four times.

Of the $^{14}CO_2$ assimilated, 402,000 dpm, 579,000 dpm and 1,034,000 dpm per plant was recovered from the 12, 20, and 30-day-old plants, respectively, after 24 hours. No significant differences in the distribution of ^{14}C were found between plants treated at 12 and 20 days (Figure 5). The main portion of the ^{14}C (79 and 75%, respectively) remained in the treated shoot while 9 and 7% was recovered from the intial root piece of 12 and 20-day-old plants, respectively. New roots imported more in plants 20 days old than in plants 12 days old, but the difference was not significant. However, 30-day-old plants retained more ^{14}C (89%) in the treated shoot. The amount of ^{14}C recovered from the initial root piece and the new roots which developed from it was significantly less than in plants which were 20 days old at the time of treatment. These observations indicate that thistles 12 days old and with leaves no longer than 3 cm are able to translocate ^{14}C-assimilates to their roots, particularly the newly developed roots on the initial root piece. The percentage of ^{14}C in the roots increased as plants reach 20 days but within 30 days of the initiation of new shoots from root pieces, the shoot competes successfully with the new roots as a sink for assimilates. After 24 hours only 8.5% of the total ^{14}C recovered was found in the roots of plants 30 days old whereas 89% was retained in the fed shoot, presumably in the apices and rapidly expanding leaves.

FIGURE 5. Distribution of ^{14}C expressed as a percent of the total recovered in 12, 20, and 30-day old Canada thistle plants, 24 hours after exposure to $^{14}CO_2$. Data plotted are means of four plants.


TREATED SHOOT
INITIAL ROOT PIECE
NEW ROOTS
^{14}C, % of total recovered
80
60
40
20
12
20
30
AGE IN DAYS

In the previous experiment, 12-day-old thistles were shown to translocate ^{14}C-assimilates following shoot exposure to $^{14}CO_2$. An experiment was set up in which 12-day-old plants were exposed to $^{14}CO_2$ for one hour and harvested 0, 3, 6, and 24 hours later. At the time of harvest, plants were separated into shoots and roots; the initial root piece and its associated adventitious roots were grouped as one in the preparation of samples. Each treatment was replicated five times.

Of the $^{14}CO_2$ assimilated, 5,600,000 dpm per plant was recovered after one hour and 1,200,000 dpm per plant at the end of the test period (Table 1). When plants were harvested after 3 and 6 hours, the ^{14}C-assimilates were retained mainly in the shoot with a small percentage present in the roots. More ^{14}C-assimilates were translocated into the roots after 24 hours (23.6%) than after 3 or 6 hours (6.8 or 8.6%).

Entry of ^{14}C-assimilates into the thistle roots was rapid, but the total amounts extracted from the plants varied (Table 1). Although translocation of ^{14}C-assimilates occurred throughout the plant system within the first hour, most of the activity was retained in the treated shoot for the first 6 hours. Twenty-three percent of the radioactivity had moved out of the treated shoot after 24 hours. These results are in agreement with the translocation pattern of assimilates in the roots of 7-week-old thistles 24 hours after exposure to $^{14}CO_2$ (Figure 4).

Ten-week-old thistles (prior to the bud stage) had the 4th, 10th, and 19th leaf from the bottom exposed to $^{14}CO_2$ to measure the potential of various leaves to export assimilates to the roots. Plants were treated at this stage because it is at this time that the maximum

TABLE 1. Recovery of ^{14}C from Canada thistle 12 days old, up to 24 hours after exposure to $^{14}CO_2$ for 1 hour.

Sampling time (hr)	^{14}C, % of total recovered*		Total dpm x 10^5 recovered	Recovery, (%)
	Treated shoot	Roots		
0 **	91.4 a***	8.6 a	56	100
3	93.2 a	6.8 a	29	51
6	91.4 a	8.6 a	23	40
24	76.4 b	23.6 b	12	22

*Figures are means of five replicates.

**Plants harvested after 1 hour exposure to $^{14}CO_2$.

***Means in the same column followed by the same letter are not significantly different at the 5% level using Duncan's Multiple Range test (16).

movement of assimilates to the roots takes place (29, 30). Treatment at a later stage results in a drain of assimilates to the flower buds. All plants had between 20 and 23 leaves at the time of treatment and reached an average height of 50 cm. The exposure chamber used in this experiment only was a sealed one pint milk bottle placed over the leaf to be treated and supported at the natural angle of the leaf with its axis. Plants were harvested after 24 hours and separated into: (1) treated leaf, (2) remainder of leaves on the stem, (3) stem, and (4) roots. In addition, treated leaves were outlined on graph paper to measure the leaf area. Of the $^{14}CO_2$ assimilated, 7,500,000 to 12,000,000 dpm per plant was recovered. Although the leaf area differed with position on the plant, there were no significant differences in the total radioactivity recovered from plants receiving the treatments (Table 2). This observation suggests that leaf area is not a major factor in the fixation of $^{14}CO_2$ and the subsequent translocation of ^{14}C-assimilates. However, plants in which the 19th leaf was treated had slightly more ^{14}C recovered than plants which had other leaves treated. A possible reason why such leaves assimilate more is the high metabolic requirements of developing leaves and their proximity to the apex rather than the area of the leaf.

The results of this experiment also indicate that in every case the majority of the radioactivity recovered (62 to 81%) was present in the fed leaf. The main portion of the ^{14}C leaving the treated shoot was recovered from the roots (7 to 19%). However, where the 19th leaf was fed, the major portion of ^{14}C apart from the treated leaf was recovered from the stem. Treatment of the 4th, 10th, and 19th leaf did not influence the distribution of ^{14}C-assimilates to the other

TABLE 2. Distribution of ^{14}C-assimilates in Canada thistle 24 hours after treatment of individual leaves with $^{14}CO_2$.

Leaf treated	Leaf area (cm^2)	^{14}C, % of total recovered*				Total dpm x 10^6 recovered
		Treated leaf	Other leaves	Stem	Roots	
4th**	38.4	81.3 a	3.0 a	5.4 b	10.2 b	8.1
10th	47.8	68.6 a	2.3 a	9.9 b	19.0 a	8.8
19th	29.0	62.3 a	4.1 a	27.0 a	7.0 b	10.3

*Figures are means of three replicates

**Leaf number with respect to spacing from the plant bottom.

leaves on the same plant. The results indicate that more ^{14}C-assimilates will be translocated to the roots if the 10th leaf was treated than from treatment of leaves above or below. Normally, leaves near the bottom export assimilates to the roots; 81.3% of the total ^{14}C recovered was present in the treated leaf 24 hours after the 4th leaf was exposed to $^{14}CO_2$. Of that exported, 10.2% went to the roots. Leaves occupying a middle position on the shoot can export assimilates in either direction; 9.9% of the total ^{14}C was recovered from the stem when the 10th leaf of treated plants was exposed to $^{14}CO_2$. When top leaves (19th) are exposed to $^{14}CO_2$, the ^{14}C-assimilates formed are concentrated in the upper part of the plant; a small portion (7%) is translocated to the roots.

The experiment showed that the ability of leaves to translocate assimilates to the roots depended to a large extent on the position they occupy on the shoot. To examine further whether the lower half of the plant is responsible to a greater extent than upper leaves for assimilate accumulation in the roots, an experiment was set up to determine whether selective defoliation of leaves had a bearing on the pattern of assimilate distribution. Six-week-old plants and 11-week-old plants with 13 and 26 fully expanded leaves, respectively, were used in this experiment. Plants were separated into two groups; each group had both growth stages. Leaves were removed; the top or bottom 6 leaves in the case of the youngest plants and the top or bottom 13 leaves in the case of older plants. The removal of leaves took place three days prior to the treatment. Plants were exposed to $^{14}CO_2$ for 10 minutes and harvested after 24 hours. Harvested plants were separated into (1) treated shoot, (2) total roots, and each treatment was replicated three times.

Of the $^{14}CO_2$ assimilated, 1,650,000 to 9,150,000 dpm per plant was

recovered. The results clearly demonstrate that translocation after treatment at the 6-week and 11-week stage (Table 3) was very similar. Most of the ^{14}C was retained in the treated shoot at both growth stages 24 hours following treatment. However, slightly more ^{14}C was retained in the treated shoot when the bottom leaves were removed, at both stages. At both growth stages the major portion of ^{14}C (87.8%) was recovered from the treated shoot; a small portion (12.2%) was recovered from the roots. In treated plants in which the top leaves were removed, less ^{14}C was retained in the treated shoot (83.9 and 79.4%) at both stages but the amount was not significantly less. The results of the experiment show that the lower half of the plant is not better able than the top half to export ^{14}C-assimilates to the roots. At the two growth stages examined the majority of ^{14}C is retained in the shoot of treated plants and only approximately 20% is exported to the roots.

In the greenhouse, the translocation of ^{14}C-labelled assimilates from a primary shoot to a number of secondary shoots was studied at two growth stages. Plants 10 weeks old, grown from 5 cm root pieces, were used in this experiment. All plants had a single shoot present on one end of the initial root piece and one major root extending from the other end. All adventitious and other lateral roots were removed before the plants were transplanted to trays. From 5 to 10 new shoots developed along this root within weeks. After 20 and 40 days the primary shoot was exposed to $^{14}CO_2$ for 10 minutes and component parts were harvested after 24 hours. Four replicates of each treatment at both stages were assayed for the presence of ^{14}C. At the time of treatment, the new shoots varied in size, but the largest leaf was 3 to 6 cm and 12 to 15 cm when plants were 20 and 40 days, respectively. The average height

TABLE 3. Distribution of ^{14}C in partially defoliated Canada thistles 6 weeks and 11 weeks old, 24 hours after exposure to $^{14}CO_2$.

Growth stage	Leaves removed	^{14}C, % of total recovered*		Total dpm x 10^5 recovered
		Treated shoot	Root	
6 weeks	bottom 6	87.8 a**	12.2 a	39
	top 6	83.9 a	16.1 a	51
11 weeks	bottom 13	87.8 a	12.2 a	48
	top 13	79.4 a	20.8 a	54

*Figures are means of three replicates.

**Means followed by the same letter in each row are not significantly different at the 5% level as determined by Students "t" test (38).

of the primary shoot was 21 cm at both treatment dates. Secondary shoots were numbered with distance from the treated shoot.

Of the $^{14}CO_2$ assimilated, 4,800,000 to 12,000,000 dpm per plant was recovered. No differences in the distribution of ^{14}C after 24 hours were found between plants treated at different growth stages (Table 4). The main portion of the ^{14}C (83 to 93%) remained in the treated shoot while 4 to 12% was recovered from the roots. The results indicate that all secondary shoots received at least some labelled assimilates. The ^{14}C-assimilates translocated to the secondary shoots were not concentrated in the smaller shoots that were expected to behave as sinks for assimilates. In almost all cases, the total ^{14}C recovered from each of the secondary shoots was one percent or less of the total amount in the plant. Of that portion of the ^{14}C translocated to the secondary shoots, there was no greater amount found in the small shoots but rather it was evenly distributed to all the shoots.

Table 4. Distribution of ^{14}C-assimilates in Canada thistle 24 hours after treatment with $^{14}CO_2$ in the greenhouse

	^{14}C recovered, % of total										
		Shoot number									
Treatment stage	Treated shoot	2	3	4	5	6	7	8	9	10	Root
	89.2	0.7	0.7	0.3	0.5	0.5	0.2	--	--	--	7.4
20	83.4	0.5	0.4	0.3	0.4	0.4	0.3	0.3	0.4	0.4	12.4
days	92.0	0.2	0.5	0.6	0.5	0.3	0.4	0.2	0.4	--	4.3
	93.0	0.3	0.7	0.3	0.2	0.2	0.2	0.1	--	--	3.8
	87.4	0.8	1.0	0.5	0.3	0.6	0.7	--	--	--	8.6
40	93.0	0.5	0.5	0.6	0.3	0.2	--	--	--	--	8.8
days	87.1	1.1	0.5	1.1	1.3	1.3	--	--	--	--	9.8
	87.6	0.7	0.7	0.9	0.4	0.5	--	--	--	--	8.7

These observations indicate that very early after the secondary shoots emerge they are no longer able to compete successfully with the rapidly growing roots for the assimilates provided by the primary shoot. Within 20 days of the initiation of new shoots, the developing roots become the key sinks for the available photosynthates in plant parts other than the treated primary shoot. The primary shoot and its various apices and meristematic regions are still the major sink for assimilates produced by that shoot and, as indicated from this study, this is the case in plants 40 days after the initiation of new shoots.

The influence of temperature on the movement of assimilates from a single primary shoot to a number of small secondary shoots was examined. To ensure the production of secondary shoots, plants for the experiment were cut back to a height of 10 cm when they were two months old. As a result there remained on each plant an average of seven fully expanded leaves. Plants were then transplanted to trays. The number of secondary shoots produced during the next three weeks varied with each plant and, therefore, the replicates were not identical. Secondary shoots sometimes appeared on lateral extensions of the initial root piece and all were connected to the original 5-cm root piece. Three sets of plants (four replicates) 11 weeks old were placed in growth chambers at constant temperatures of 10°C±1, 20°C±1, and 27°C±1. The primary shoot was immediately exposed to $^{14}CO_2$ for 10 minutes and the whole plant was harvested 24 hours later for ethanol extraction. All plants were grown in a growth chamber at 20°C±1 prior to the treatment.

Of the $^{14}CO_2$ assimilated, 1,450,000 to 2,100,000 dpm per plant was recovered. Of that portion of ^{14}C-assimilates which left the treated shoot, there was significantly more ^{14}C recovered from the roots in

plants at 10°C than at either of the two higher temperatures (Table 5). The majority of the ^{14}C was recovered from the $^{14}CO_2$-fed shoot, although more was retained at 27°C than at 10°C. The results indicate that a rise in temperature from 20°C to 27°C had no effect in terms of the assimilate distribution pattern. At all three temperatures, very little of the labelled assimilates was translocated to the secondary shoots. Because there was very little ^{14}C recovered in each secondary shoot, the data were pooled for each plant. Assimilates exported from treated shoots were divided equally between secondary shoots and roots, except at 10°C where the roots were acting as prominent sinks.

Table 5. Recovery of ^{14}C from Canada thistles 24 hours after exposure to $^{14}CO_2$ at three temperatures

Temperature	^{14}C, % of total recovered*			Total dpm x 10^5 recovered
	Treated shoot	Secondary shoots	Roots	
27°C	96.0 a**	1.5 a	2.5 b	21.5
20°C	93.5 ab	3.5 a	3.0 b	14.3
10°C	91.1 b	3.4 a	5.6 a	19.6

*Data are means of four replicates

**Means in the same column followed by the same letter are not significantly different at the 5% level using Duncan's Multiple range test (16).

An experiment was carried out to determine if there was reciprocal transport of assimilates taking place between the primary shoot and the end shoot of a number of secondary shoots arising from the root. In this case it was desirable to have a number of secondary shoots and, in

addition, to have them all on the same root piece rather than on lateral extensions of a common root piece. Plants which had only one shoot present on a 30 cm root piece after five weeks in the greenhouse were selected for this experiment. Such plants were then placed outdoors for an additional five weeks during which time a number of new shoots developed along the root piece. The period specified outside the greenhouse occurred from mid-August to late September during which time day temperatures were between 20°C and 24°C; night temperatures sometimes went as low as 14°C. The experiment was comprised of two treatments: (1) treating the primary shoot with $^{14}CO_2$ and determining the radioactivity in roots and secondary shoots, and (2) treating the end shoot of the new shoots formed. All plants were exposed to $^{14}CO_2$ for 1 hour outdoors and harvested after 24 hours. Each treatment was replicated four times. All shoots present were numbered; #1 was the initial primary shoot, while the secondary shoots were numbered consecutively with distance from #1. The 30-cm root piece was divided into three equal sections for convenience of handling and buds appearing on these sections were included for quantitative assay.

The distribution of radioactivity in the shoots is shown in Table 6, and that in the root sections in Table 7. Of the $^{14}CO_2$ assimilated, 902,000 to 10,125,000 dpm per plant was recovered. The data from the plants receiving the two treatments showed greater variability within the treatments and, as a result, any significant trends may be hidden (Table 6). The largest portion of the radioactivity apart from the treated shoot was recovered from the roots. In every case, ^{14}C was detected in each of the secondary shoots, although the amount of ^{14}C expressed as a percentage of the total recovered was very low.

Table 6. Distribution of ^{14}C-assimilates in primary and secondary shoots of Canada thistle 24 hours after treatment with $^{14}CO_2$.

		^{14}C recovered, % of total									
			Secondary Shoot No.*								
	Plant No.	Primary shoot	2	3	4	5	6	7	8	9	10
1° sh. treated	1.	*75.8***	.2	.2	.1	.3					
	2.	*77.6*	.4	.2	.01	.01	.01				
	3.	*71.8*	.1	.02							
	4.	*64.1*	.1	.03	.03	.01	.03				
2° sh. treated	5.	.8	.3	1.02	.4	.3	.5	1.5		15.2	*58.9*
	6.	.03	.01	.2	.3	.6	*40.0*				
	7.	.8	.5	.5	1.3	*78.9*					
	8.	.7	.6	4.5	*45.7*						

*Numbered with distance from initial primary shoot

**Numbers in Italics denote treated shoots.

Table 7. Distribution of ^{14}C-assimilates in sections of 30 cm root segments of Canada thistle 24 hours after treatment with $^{14}CO_2$.

	^{14}C recovered in the root, % of total					
	Root section*					
	Proximal**		Middle		Distal	
Plant No.	Root	Buds	Root	Buds	Root	Buds
1	12.6	7.7	2.5	.4	.2	.01
2	18.3	3.3	.04	.1	.03	--
3	14.5	11.7	1.7	.04	.1	.04
4	32.1	1.2	1.9	.4	.1	--
5	16.8	1.2	2.08	.5	.5	--
6	41.6	10.9	1.8	3.3	1.4	--
7	9.7	--	5.5	2.1	.7	--
8	10.0	4.6	30.1	2.7	.8	.3

*Each segment was 10 cm in length; **Segment description with respect to the treated shoot.

With few exceptions, the amount of ^{14}C recovered from a secondary shoot was less than 1 percent of the total. In plant #5, however, the secondary shoot adjacent to the treated end shoot received 15.2% of the recovered radioactivity. In general, it was found that the percentage of the radioactivity in secondary shoots decreased with increased distance from the treated end shoot. In every case ^{14}C was detected in the primary shoot 30 cm from the treated end shoot; in one instance (Plant #6), the amount was negligible. This observation indicates that there is reciprocal transfer of ^{14}C-assimilates between primary shoots and small daughter shoots present on the same root section. The end shoot is not only capable of meeting its own assimilate needs but is also able to send assimilates to the roots and to a limited extent to neighboring shoots on the same root.

Of the ^{14}C recovered from the roots, the major portion was found in the 10-cm section closest to the treated shoot. This was true in the case where the primary shoot was treated and also where the end secondary shoot was treated. Less ^{14}C was recovered from the middle segment and least from the section farthest from the fed shoot. Although the actual percentage of ^{14}C found in the root piece was greater than that in accompanying root buds when present, the buds had four times the amount of radioactivity when expressed on a per gram fresh weight basis. This is to be expected since growing buds are very active metabolically. Although the term bud has been used, they more closely resemble etiolated shoots with an average height of 1.5 cm. Although most of the root sections had an average of three such buds, there were cases in which nine buds appeared on one section. The secondary shoots were all under 6 cm in height and each had a fresh weight of between 0.4 and 0.9 grams.

Feeding experiments in the field were set up to examine reciprocal transfer of ^{14}C-assimilates between a primary and a secondary shoot present on the same root piece. The root piece was 5 cm long and the secondary shoot was smaller in height and leaf stage than the primary shoot. The primary shoot had eight fully expanded leaves and the one secondary shoot six leaves at the time of treatment. Plants were exposed to $^{14}CO_2$ for 10 minutes, seven and nine weeks after being transplanted to the field, and they were harvested after 24 hours. Each treatment was replicated three times.

The amount of ^{14}C recovered from field-treated plants was considerably lower than from plants treated in the greenhouse. Of the $^{14}CO_2$ assimilated, 170,000 to 780,000 dpm per plant was recovered. Reciprocal transfer of ^{14}C-assimilates was shown to take place between the primary shoot and the secondary shoot at both stages examined (Table 8). Treatment of the primary or the secondary shoot did make a difference in the pattern of distribution of ^{14}C-assimilates in plants seven weeks old. The majority of ^{14}C recovered was confined to the treated shoot (82.7 and 92.6%), but of the ^{14}C exported from the fed portion, the largest portion (14.8 and 6.8%) went to the roots. A small portion (2.5 and 0.6%) was recovered from the untreated shoot. This was true not only when the primary shoot was fed but also when the secondary shoot was treated. When the primary shoot was treated in 7-week-old plants, significantly more ^{14}C was exported to the roots than when the secondary shoot was fed under the same conditions. As much as 2.5% of the total ^{14}C recovered was found in the secondary shoot. If the secondary shoot was fed, however, less than one percent was translocated to the larger primary shoot. The results indicate that at this stage

reciprocal transport is possible but the smaller shoot retained almost all of the $^{14}CO_2$ assimilated rather than exporting the ^{14}C-assimilates to the roots and the other shoot.

Table 8: Percent ^{14}C recovered from thistles 24 hours after exposure to $^{14}CO_2$ in the field at two growth stages.

Growth stage	Shoot treated	^{14}C, % of total recovered*		
		Treated shoot	Roots	Untreated shoot
7 weeks	1°	82.7 b**	14.8 a	2.5 a
	2°	92.6 a	6.8 b	0.6 b
9 weeks	1°	89.1 ab	9.7 ab	1.2 ab
	2°	84.1 ab	12.7 ab	3.2 ab

*Figures are means of three replicates

**Means followed by the same letter in each column are not significantly different at the 5% level as determined by Student's "t" tests (38).

Most of the ^{14}C assimilated was retained in the treated shoots of plants exposed to $^{14}CO_2$. Of the ^{14}C exported from the treated portion, most was recovered from the roots and least from the secondary shoots appearing on the root system. An experiment was set up in the field to determine whether the presence or absence of secondary shoots would influence the export of ^{14}C-assimilates to the roots when the primary shoot was treated. Two-month old plants with a single shoot 20cm tall were compared with plants which had two to four secondary shoots in addition to the primary shoot. Both treatments included exposing only the primary shoot to $^{14}CO_2$ for 10 minutes and harvesting the treated shoot and the untreated portion of the plant after 24 hours.

Because ^{14}C recovery for secondary shoots represent less than one percent of the total recovered per plant, the data for secondary shoots were pooled with those of the root. Each treatment had four replicates (plants) and the experiment was repeated after a two week interval. The experiment then was not designed to determine how much ^{14}C was translocated to the additional shoots but rather to determine if the presence of secondary shoots influenced the pattern of ^{14}C-assimilate distribution in treated plants.

Of the $^{14}CO_2$ assimilated, 808,000 dpm to 4,530,000 dpm per plant was recovered. No significant difference in the distribution of ^{14}C after 24 hours was found between plants treated at different dates (Table 9). More ^{14}C was retained in the treated shoot of plants with secondary shoots (85.0 and 81.5%) than in plants without secondary shoots (78.0 and 80.5%) but the difference is not statistically significant.

Table 9. Distribution of ^{14}C-assimilates in Canada thistles with and without secondary shoots 24 hours after treatment with $^{14}CO_2$ in the field.

		^{14}C recovered, % of total*	
	Secondary Shoots	Treated shoot	Root
August 20	present	85.0 a**	15.0 a
	absent	78.0 a	22.0 a
Sept. 5	present	81.5 a	18.5 a
	absent	80.5 a	19.5 a

*Data are mean of four replicates.
**Means followed by the same letter in each column are not significantly different at the 5% level as determined by Student's "t" test (38).

The results of the experiment emphasize that the roots act as sinks for the available ^{14}C-assimilates not retained in treated shoots. If secondary shoots were not present on these roots, there would not be a significant increase in the amount of ^{14}C found in the roots.

In the field, rosettes of thistles formed late in the growing season were examined with respect to the translocation of ^{14}C-assimilates after exposure to $^{14}CO_2$. Ten-day-old thistles grown from 15-cm root pieces in the greenhouse were transplanted to the field on May 24. In the following three months, an additional three to seven secondary shoots emerged from the original root piece. On August 24, all plants were placed into one of two groups and the secondary shoots were cut back to ground level. In one group, the primary shoot (at flowering stage) was also cut back but in the other group it was left intact. In the following month not only did a number of new rosettes develop from the roots, but also leaves appeared on the previously cut secondary shoots. For convenience, and to prevent confusion with the new shoots (rosettes) the secondary shoots were assigned the term "regrowth shoots". The largest of the rosettes formed was exposed to $^{14}CO_2$ on Sept. 24 for one hour and the distribution of labelled assimilates was noted in untreated plant parts after 24 hours.

Out of the twelve plants examined in the experiment, eight which were considered representative were selected to demonstrate the results in Table 10. Of the $^{14}CO_2$ assimilated, 4,130,000 dpm to 13,110,000 dpm per plant was recovered. Some variability in the distribution of ^{14}C occurred between replicates of both treatments but, nevertheless, certain trends are apparent. In every case the majority of the labelled assimilates was recovered from the treated rosette. In some instances

Table 10. Distribution of ^{14}C-assimilates in Canada thistle 24 hours after treatment with $^{14}CO_2$ in the field.

		^{14}C recovered, % of total*				
	No.	Treated rosette	Roots	Other rosettes	Regrowth shoot(s)	Primary shoot
Primary shoot present	1	93.2	5.7	.1	1.0	.01
	2	99.2	.2	.02	.5	.03
	3	98.4	1.1	--	.3	.11
	4	98.1	1.1	.04	.7	.1
Primary shoot removed*	5	98.4	0.5	.9	.1	--
	6	80.03	7.5	11.5	1.4	--
	7	87.7	10.9	2.2	.1	--
	8	96.9	2.5	.3	.3	--

*Primary shoot removed along with secondary shoots 1 month prior to treatment.

less than one percent of the total recovered was found in the remainder of the plant. When the primary shoot was left intact, treatment of the largest new rosette resulted in a preferential transport of ^{14}C to the roots and the regrowth shoots. Trace amounts of ^{14}C (.01 to 0.1%) were detected in the primary shoot of the same plant even though the distance between it and the treated rosette may have exceeded 50 cm. The other rosettes received as much ^{14}C (0.02 to 0.1%) as the primary shoot but less labelled assimilates than the regrowth shoots. The largest portion of ^{14}C outside the treated rosette was found in the roots (0.2 to 5.7%). Treated plants in which the primary shoot was removed one month prior to treatment gave evidence of a different distribution pattern. In such cases the other rosettes contained a higher percentage of recovered ^{14}C than the regrowth shoots, with one exception (plant No. 8). The results indicate that 1-month-old rosettes are capable of exporting assimilates even though the meristematic regions of the treated rosette retain the bulk of the ^{14}C-assimilates. The largest of the new rosettes sends assimilates to the regrowth area but little if any of the available ^{14}C-assimilates is transported to other rosettes. It is difficult to ascertain to what extent the primary shoot plays a role in assimilate supply to these regrowth shoots. The results do show, however, that when the primary shoot is absent treatment of a rosette results in the accumulation of ^{14}C primarily in the root (0.5 to 10.9%) and in the other rosettes (0.3 to 11.5%). A small portion of ^{14}C (0.1 to 1.4%) was found in the regrowth shoots.

Translocation of ^{14}C-assimilates in leafy spurge

In order to examine the growth stage at which leafy spurge plants first translocate assimilates to the roots, an experiment was set up in the greenhouse with 16-day-old, 35-day-old, and 57-day-old plants. The height of the shoot at each of these growth stages was 5 cm, 11 cm, and 20 cm, respectively. The plants were exposed to $^{14}CO_2$ for 10 minutes and harvested 6 hours following the treatment. Each treatment was replicated three times. At the time of harvest, each plant was separated into (1) treated shoot and (2) roots. Of the $^{14}CO_2$ assimilated, 275,500, 2,925,000 and 5,625,000 dpm per plant was recovered from plants treated at the three growth stages. Sixteen-day-old plants showed a high degree of variability in recovery data, from 165,000 dpm to 357,000 dpm per plant. Considerably less variability was observed among replicates of the 35-day-old and 57-day-old plants.

In all cases the treated shoot retained most of the assimilated radioactivity (Table 11). Treatment of the plants at the different

TABLE 11. Percentage of total ^{14}C recovered from roots and shoots of leafy spurge 6 hours after exposure to $^{14}CO_2$ at different growth stages.

Growth stage (days)	^{14}C, % of total*		Total dpm x 10^4 recovered
	Treated shoot	Roots	
16	95.5 a**	4.5 a	26
35	95.7 a	4.3 a	293
57	91.6 b	8.4 b	563

*Figures are means of four replicates.

**Means in the same row followed by the same letter are not significantly different at the 5% level using Duncan's Multiple Range test (16).

stages did influence the relative distribution of ^{14}C-assimilates. Plants which were approximately 2 months old (57-day-old plants) accumulated significantly more ^{14}C-assimilates in the roots (8.4%) than did plants which were treated at either of the two other stages. Sixteen-day-old and 35-day-old plants translocated 4.5 and 4.3%, respectively, of the ^{14}C-assimilates to the roots. There was no significant difference in the behavior of the 16-day-old and 35-day-old plants.

From this experiment it was evident that translocation from a treated shoot to the roots takes place rapidly and that differences could be detected in the amount of ^{14}C accumulated in the roots after only 6 hours, at the growth stages examined. The experiment was repeated after three days and a number of changes were made. The period of exposure to $^{14}CO_2$ was extended from 10 minutes to 1 hour and the period before plants were harvested was extended from 6 hours to 24 hours. Only 19-day-old plants and 60-day-old plants were included in this experiment. Data presented in Table 12 indicate that treatment of plants and harvest after 24 hours did influence the pattern of distribution of ^{14}C-assimilates.

TABLE 12. Percentage of total ^{14}C recovered from leafy spurge plants 24 hours after exposure to $^{14}CO_2$ at two growth stages.

Growth stage (days)	Height of shoot (cm)	^{14}C, % of total*		Total dpm x 10^4 recovered
		Treated shoot	Roots	
19	5	90.0 a**	10.0 b	149
60	20	79.7 b	20.3 a	692

*Figures are means of four replicates.

**Means followed by different letters in the same column are significantly different at the 5% level as determined by the standard "t" test (38).

Only 10% of the total ^{14}C recovered from the treated plants was found in the roots of plants 19 days old whereas plants 60 days old accumulated twice as much in the roots (20.3%) after 24 hours.

Leafy spurge plants 2 months old were exposed to an atmosphere of $^{14}CO_2$ for 1 hour and harvested immediately and after 1, 3, and 6 hours. Of the $^{14}CO_2$ assimilated, 16,960,000 dpm per plant was recovered at the end of the exposure period (Table 13). The total dpm recovered per plant decreased rapidly during the test period. No explanation is offered why the amount of ^{14}C recovered should undergo a three-fold decline in 6 hours. The distribution of ^{14}C-assimilates at 0 hr and 1 hr was identical; less than one percent was recovered from the initial root piece (5 cm) and the roots developing from it. In plants harvested after 3 hours again the major portion of ^{14}C was present in the treated shoot.

TABLE 13. Recovery of ^{14}C from 6-week-old leafy spurge plants after exposure to $^{14}CO_2$.

Sampling time (hr)	^{14}C, % of total*			Total dpm x 10^6 recovered	% loss**
	Treated shoot	Initial root piece	Remaining roots		
0	99.97 a***	.01 a	.02 a	16.9 a	0 a
1	99.97 a	.01 a	.02 a	13.1 b	22 b
3	98.53 a	.53 b	.94 b	12.8 b	24 b
6	92.76 b	.86 b	6.38 c	5.2 c	69 c

*Figures are means of three replicates.

**Loss of ^{14}C expressed as a percent of the amount recovered at 0 hr.

***Means in the same column followed by the same letter are not significantly different at the 5% level using Duncan's Multiple Range Test (16).

Most ^{14}C recovered from plants harvested after 6 hours, apart from the treated shoot, was found in the actively growing roots (6.38%). Such roots are considered the major sink for the available assimilates. Less than one percent of the total ^{14}C present was recovered from the original 5 cm root piece.

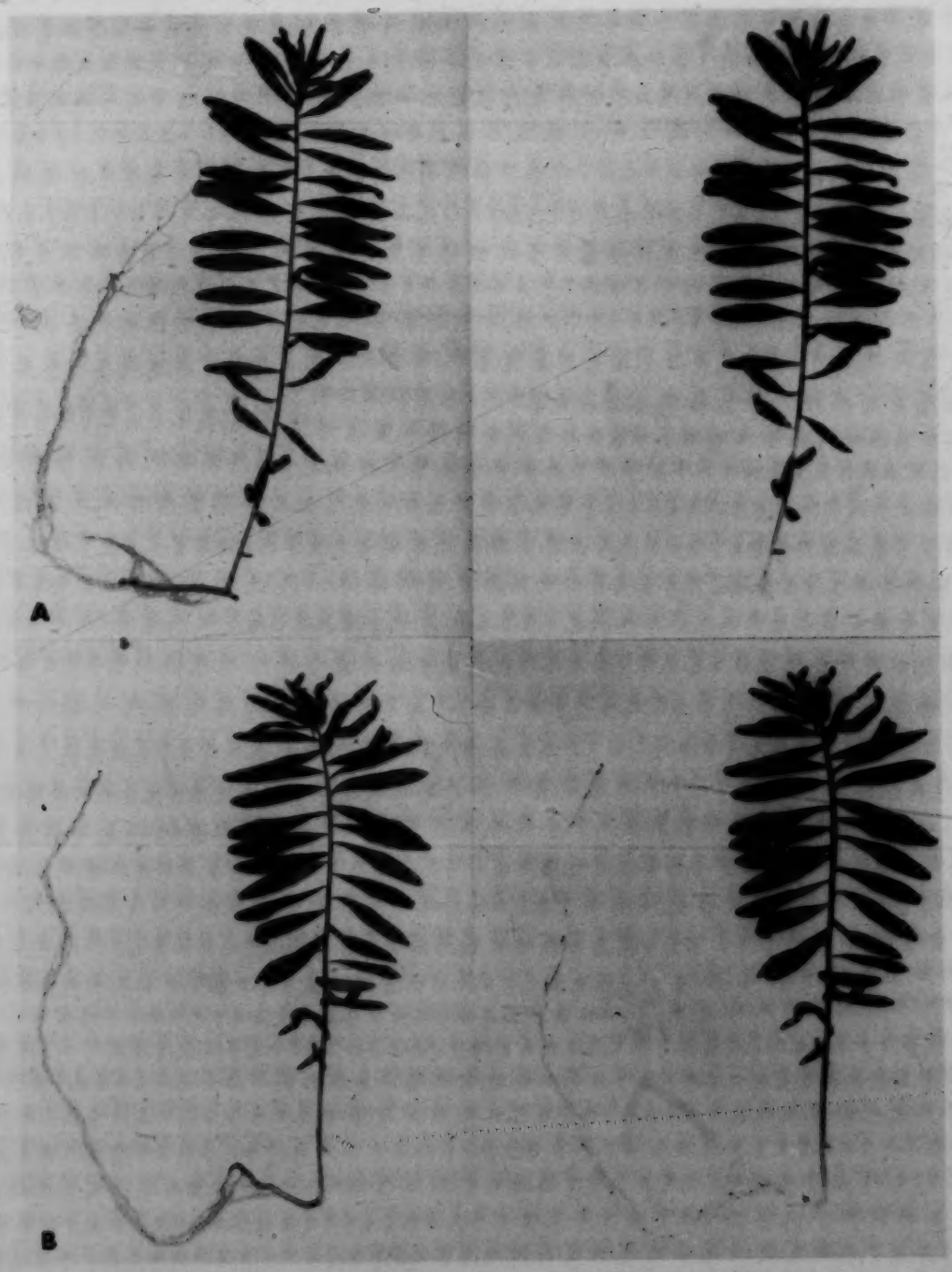
Plants from all sampling times were autoradiographed. Figures 6 and 7 consist of autoradiographs and mounts of plants harvested at 0, 1, 3, and 6 hours following treatment. The small amount of activity going to the roots was detected only with difficulty by autoradiography. Most of the radioactivity was present in the treated shoot. Within the treated portion, the label was evenly distributed throughout the entire shoot; apices did not have a greater accumulation of ^{14}C than the older bottom leaves. Plants which had translocated assimilates for 1 hour had no more label in the roots (Fig. 6B) than plants which had been harvested at 0 hours (Fig. 6A). The small amount of ^{14}C present in roots of plants harvested 0, 1, and 3 hours following treatment was detected by quantitative analysis but did not show up on the autoradiographs. Figure 7B shows some label in the roots 6 hours following treatment. Of the radioactivity in the roots, most was concentrated in the buds. The autoradiographs illustrated in Figures 6 and 7 are in agreement with the corresponding data from plants that were ground and extracted at the various sampling times. The results show that translocation to the roots does take place between 3 and 6 hours following treatment. Developing buds on the roots were acting as prominent sinks.

An experiment was carried out to determine whether ^{14}C-assimilates would continue to go to the major sink areas if the buds had developed into leafy aerial shoots. To ensure the production of secondary shoots,

FIGURE 6. Distribution of ^{14}C-assimilates in 2-month-old leafy spurge plants, (A) 0 hr and (B) 1 hr after exposure to $^{14}CO_2$ for 1 hour. Labels appear beside plant mounts. Autoradiographs are located to the right hand side of the figure.

A
B

FIGURE 7. Distribution of ^{14}C-assimilates in 2-month-old leafy spurge plants, (A) 3 hr and (B) 6 hr after exposure to $^{14}CO_2$ for 1 hr. Labels appear beside aplant mounts. Autoradiographs are located to the right hand side of the figure.


A
B

leafy spurge plants, 3 months old, were cut back to ground level and allowed to regrow. Within 3 weeks, new shoots developed at the base of the former primary shoot and a number of smaller secondary shoots developed from the roots. Three weeks from the date of the initial clipping, plants were exposed to $^{14}CO_2$ for one hour and harvested immediately and after 24 and 48 hours. Each treatment was replicated five times; three replicates (plants) were ground and extracted with ethanol and two replicates were used for autoradiographs.

The data for ^{14}C present in the secondary shoots were pooled. Of the $^{14}CO_2$ assimilated, 38,200,000 dpm per plant was recovered immediately after the exposure period and 12,900,000 dpm per plant was recovered at the end of the test period. The distribution of assimilates was the same at the 48 hour harvest as at 24 hours (Table 14). In all cases, the treated shoot contained most of the assimilated radioactivity.

TABLE 14. Recovery of total ^{14}C in roots and shoots of leafy spurge plants 24 and 48 hours after exposure to $^{14}CO_2$.

Sampling time (hr)	^{14}C, % of total*			Total dpm x 10^6 recovered	% loss**
	Treated shoot(s)	Roots	Secondary shoots		
0	100 a***	0 b	0 c	382	0 a
24	75.2 b	24.4 a	0.4	297	22 b
48	72.1 b	27.8 a	0.1	129	68 c

*Figures are means of three replicates.

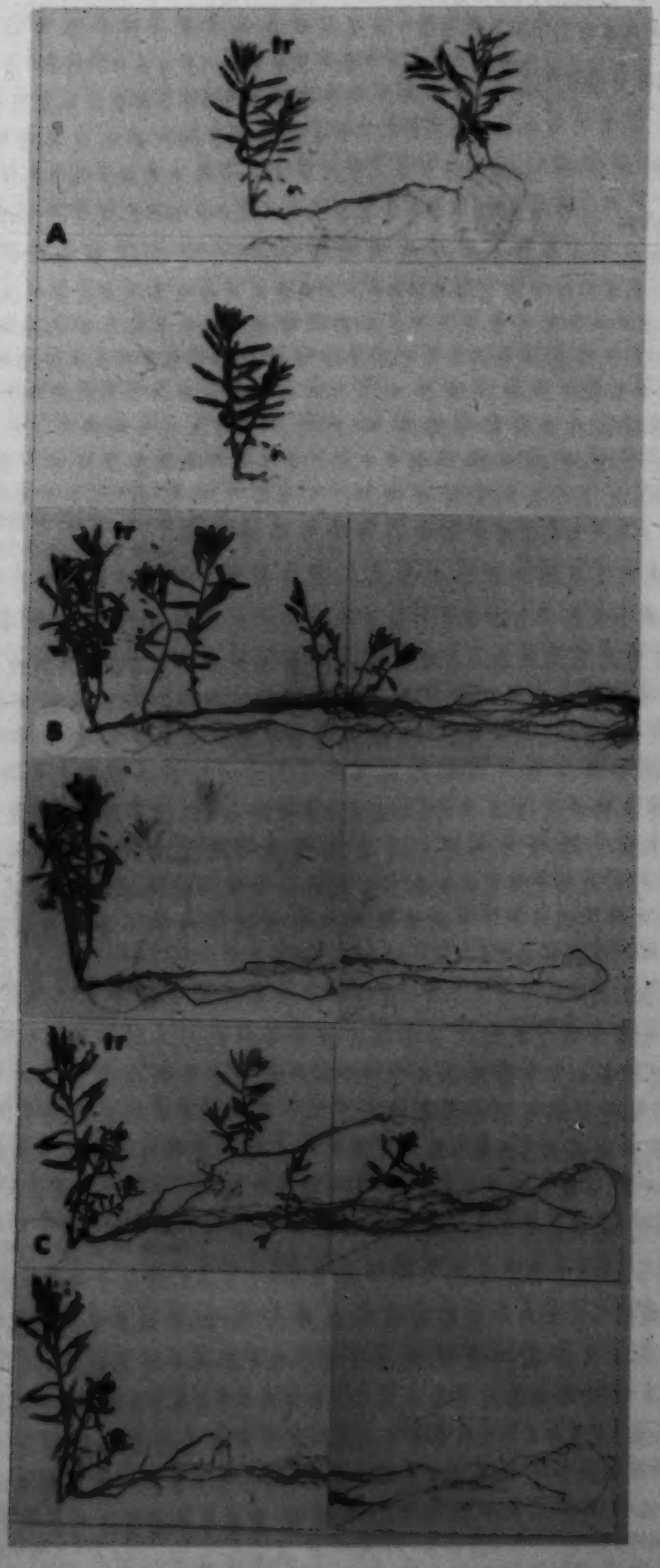
**Loss of ^{14}C expressed as a percent of the amount recovered at 0 hr.

***Means which are in the same row followed by the same letter are not significantly different at the 5% level using Duncan's Multiple Range Test (16).

Of that which left the treated shoot, most was recovered from the roots (24.4 and 27.8%) and a very small amount (0.4 and 0.1%) from the secondary shoots. There was a substantial difference in the total amount of ^{14}C recovered from plants harvested after 24 and 48 hours.

The quantitative observations were borne out by the autoradiographs (Fig. 8). The shoot supplied with $^{14}CO_2$ always retained most of the radiocarbon it fixed. The concentration of ^{14}C was lower in the secondary shoots than in the part of the root from which they emerged. The main shoot supplied ^{14}C-assimilates to all secondary shoots of plants harvested after 24 hours but in plants harvested after 48 hours, ^{14}C was supplied only to the roots. Figure 8B shows that ^{14}C-assimilates are present in untreated shoots. Secondary shoots some distance from the treated main shoot showed only a trace of radioactivity. At both sampling times, the root system was extensively labelled with radiocarbon, with some of the roots labelled more heavily than others. There was also localization of the ^{14}C at the root and secondary shoot apices. The ^{14}C in the importing secondary shoots was localized in the young expanding leaves. Control plants (Fig. 8A) did not contain detectable quantities of radioactivity beyond the treated portion.

FIGURE 8. Distribution of ^{14}C-assimilates in 15-week-old leafy spurge plants (A) o hr, (B) 24 hr and (C) 48 hr after exposure to $^{14}CO_2$ for 1 hr. Labels appear beside plant mounts. Autoradiographs are situated below the plant mounts in the figure.


A
B
C

Microtechnique:

Sectioned material and cleared whole tissues indicate that the connections between the vascular systems of the root and shoot for Canada thistle and leafy spurge are in many respects similar. The anatomical feature which appears to be significant with respect to the junction is the uninterrupted extension of two collateral bundles with endarch xylem from the protoxylem poles of the root stele to the shoot. The two vascular traces are physically separated by a wide band of parenchyma cells and later diverge in the shoot to form additional vascular bundles.

The characteristic features of Canada thistle root and shoot anatomy can be readily distinguished in Fig. 9A. The micrograph illustrates the median longitudinal section of the shoot at the point of union with the root. The root stele (RS) is located to the right of the photograph and the shoot is situated at the extreme left. The xylem arrangement of the root is diarch with two main parenchyma rays and a number of smaller, narrower rays. The vessel members are scattered among the more numerous thick-walled fibres. The phloem (Ph) forms a fan-shaped area on either side of the secondary xylem. The cortex (Co) consists of many layers of more or less spherical parenchyma cells and is very well developed. The examination of the stem anatomy was restricted to the basal region of the shoot. The most notable feature here was the collateral bundles separated by a ray of parenchyma cells. In some of the material examined, lateral roots extended from the area of the junction but this did not occur in the majority of cases. The observed anatomy of both root and shoot is in agreement with earlier

FIGURE 9. A. Light micrograph of the median longitudinal section of Canada thistle shoot present on the root. A continuum of vasculature (V) extends from the shoot on the left to the root stele (RS) near the center. Note in the root, the diarch xylem arrangement with phloem (Ph) on either side and the well developed cortex (Co). An unmarked arrow denotes the site of transition between the root and shoot vasculature. Section is 15 µm thick. Bright field. X40.

B. Light micrograph of vasculature transition zone in Canada thistle. The shoot viewed in a longitudinal plane is found to the left of the photograph. The root vasculature is located to the right (slightly out of focus) and is viewed in a transectional plane. Perforation plates (PP) are denoted at the ends of individual vessel members (VM). Section is 15 µm thick. Bright field. X256.

RS
VM
VM

reports (35, 45), and the micrograph illustrated is representative of the material examined.

The median trace consists of two bands of xylem continuous with the protoxylem poles of the root and is bordered by phloem groups. Each of the two vascular traces is collateral consisting of an inner strand of endarch xylem and an outer strand of phloem. There is a distinct separation between the two bundles and the central core in the shoot is directly opposite one of the two main parenchyma rays of the root. This core area extends the distance of the shoot and forms a wedge-shaped notch in the secondary xylem of the root. The point where the shoot vasculature unites with the stele of the root (unmarked arrow in Fig. 9A) is enlarged in Fig. 9B. A transectional view of the root tracheary elements, to the right and slightly out of focus, can be seen only with difficulty. However, what can be distinguished are the numerous vessel members extended longitudinally in the shoot, continuous with the vessels present in the root. Immature and not yet fully differentiated vessel members are located near the bottom of the micrograph. Two perforation plates are prominent in this micrograph. Individual vessel members appear to vary in both length and width. The vessels closest to the root, shorter and more compact, are viewed in an oblique plane. Because of the thickness of the section (15 μm) and the depth of field, these individual vessel members only appear shorter. Such cells probably are modified structurally or distorted somewhat with the change that is taking place at this point. The strand of vessels has been twisted to accommodate its orientation with the vasculature of the root. The continuum described represents a root-to-shoot "transition". Esau (15) defined the region of a

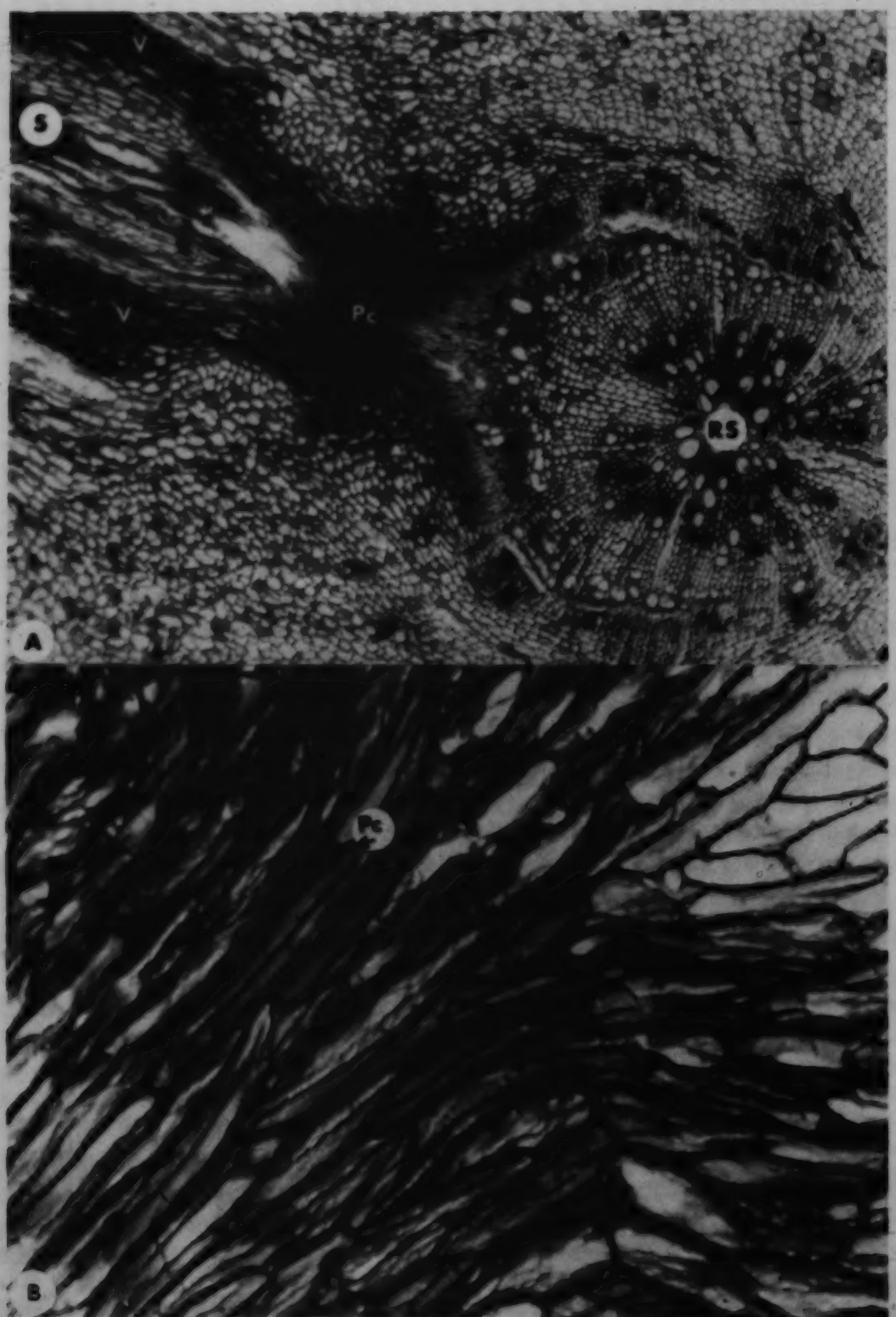
seedling where structural details change between the root and shoot system as the "transition zone" or "transition region", and the area described here cannot be termed transition zone in that same sense.

Hamdoun (25) reports that shoot buds appearing on the roots of Canada thistle have a pericyclic origin and arise centrifugally from the protoxylem poles of the root. In the shoot then, xylem differentiates from the center of the vascular cylinder towards the periphery. In the root, the opposite is true; the least mature are located on the outside and the most mature vessel members are found near the center. For the vessels to be continuous from the shoot to their counterparts in the root, some spatial shifting of the vessel members must take place. It is difficult to actually pinpoint the site of the protoxylem poles. Secondary growth of tissues causes tremendous strain on the protoxylem poles and other primary tissue to the extent that the protoxylem poles collapse. However, the collateral strands in this instance extend to the root stele and an area which approximates that of the protoxylem poles.

In sections from the same piece of material taken approximately 375 µm on either side of the median trace, there was evidence of a wide area, entirely of procambial cells, which separates the shoot from the root stele (Fig. 10A & B). At the base of the shoot (on the left in the photograph) the vasculature is evident. However, no evidence of fully differentiated tracheary or phloem elements was present. Acropetally differentiated tracheary elements of the shoot were observed as isolated vessel members in the area between the strands. In addition, some of the cells outside the area of the xylem appeared to be phloem but no evidence of fully differentiated sieve tube elements

FIGURE 10. A. Light micrograph of root-shoot vasculature of Canada thistle in sections taken 375 µm on either side of the median section. A wide area of procambium (Pc) forms a gap between the vasculature (V) of the shoot (S) and that of the root stele (RS). Section is 12 µm thick. Bright field. X40.

B. Light micrograph of the area of procambial cells located at the base of the shoot which separates the vasculature of the shoot and the root. Each procambium (Pc) cell is densely cytoplasmic and elongate at the onset of differentiation but no mature vascular tissue is present. Section is 12 µm thick. Bright field. X256.


S
V
V
Pc
RS
A
RS
B

was found.

The procambial connection is obvious, appearing as a gap between the vasculature of root and shoot. There is no mature vasculature in this area. The differentiation of tracheary elements in this region was conspicuous, however (Fig. 10B). Each procambial cell is still undifferentiated and continues to elongate. The procambial cells by and large gave evidence of increased protoplast stainability. The endarch maturation of the collateral bundles is offered as a possible explanation why this area, which will eventually link root and shoot, has a lack of fully differentiated tracheary elements. Mature vasculature is present in the median longitudinal section because in the developmental sequences of vasculature initial xylem and phloem are formed here. On either side of the median the least mature tracheary elements (i.e., most recent cambial derivatives) are laid down. Such cells are viewed as elongated procambium. As the process of secondary growth continues over time, these cells differentiate into either phloem or xylem and become functional. Sections taken even further from the median and towards the periphery of the shoot indicate a lack of procambial cells. In such sections only cortical parenchyma cells are found in the area separating the vasculature of the root and the shoot. The results of this study indicate that the maturation of vasculature proceeds from the center of the shoot and that there is a definite continuum between the root and shoot in the median longitudinal section.

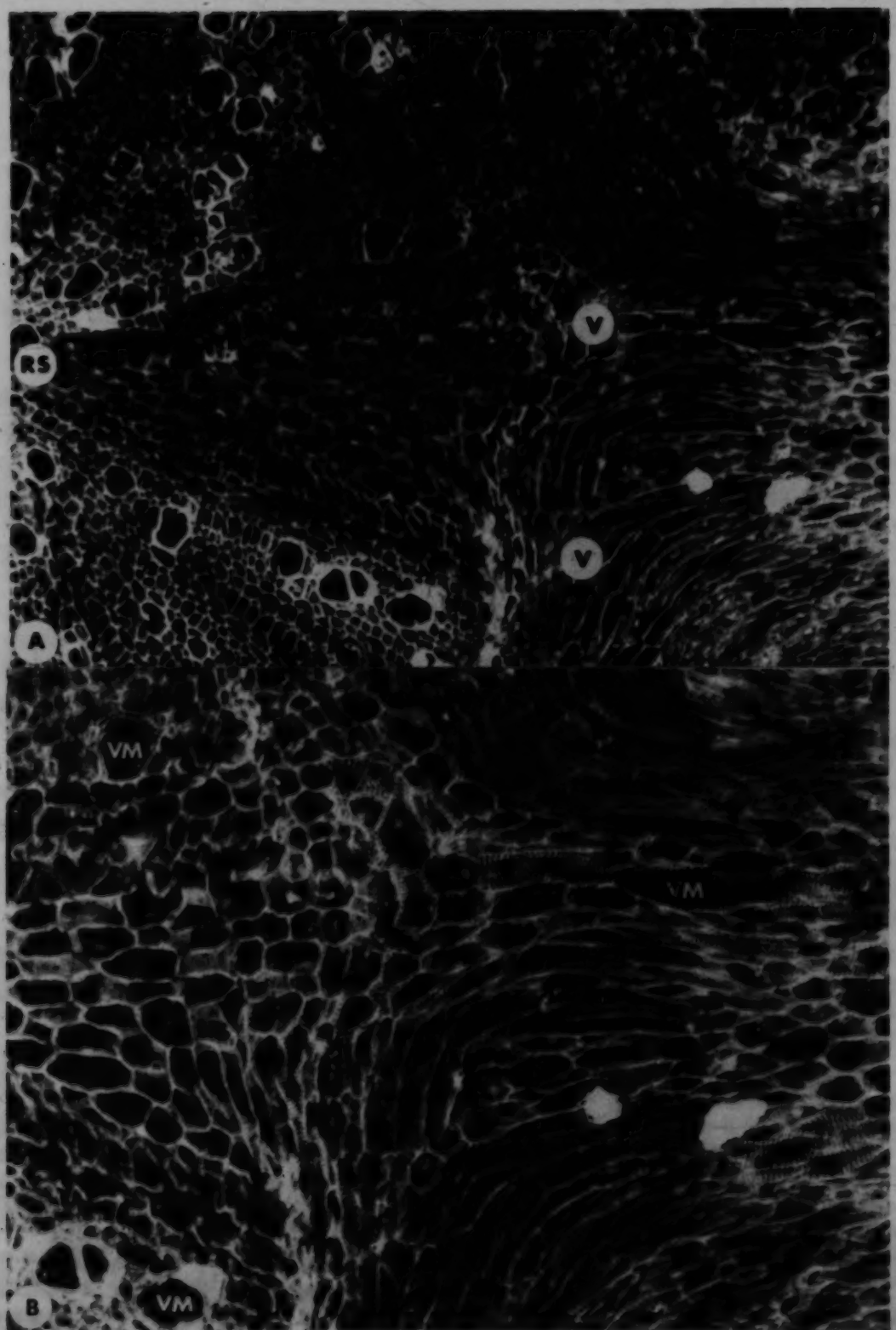
The prominent features of leafy spurge root and shoot anatomy are shown in Fig. 11 A & B. Although the micrographs primarily depict the junction of the root with the shoot, the general anatomy of both

the root and the shoot can be seen as well. In the material examined the observed xylem arrangement of the root was triarch and it is reported as the most common. Reports in the literature have indicated that pentarch, tetrarch (5, 51) and diarch (45) xylem arrangement also occur. Secondary growth in the root is prolific, resulting in a strongly developed cylinder, and is not limited as is the case in thistle. The vessel members are few in number and are found in rows radiating from the center. These xylem vessels along with the numerous thick-walled tracheids comprise two thirds of the diameter of the root. Quite often secondary growth continues to the extent that only a single parenchyma layer separates the xylem arms. Theoretically this should aid in determining xylem arrangement and help to localize primary and secondary xylem elements. In actual fact, the central area becomes a solid core of dead tissue and identifying features become particularly difficult to find. The remaining one third of the root is comprised of parenchyma associated with phloem and a cork layer which is highly suberized. Leafy spurge has a continuous ring of pericyclic cambium and, therefore, should be able to give rise to lateral organs (roots or shoots) anywhere on the circumference of that circle. In the roots under study, however, laterals generally arose opposite the protoxylem poles.

The micrograph in Fig. 11A illustrates the collateral bundles extending from the shoot to the root. The root stele occupies the left hand side of the photograph. Vessel members (VM) seen both in transection and along their length are detected with some difficulty in this section taken at the axis of root and shoot (Fig. 11B). A continuum can be seen, nevertheless, which provides an uninterrupted

FIGURE 12. A. Light micrograph indicating starch distribution in the median longitudinal section of leafy spurge. Vasculature (V) occuping the center of the photograph lies between the shoot (S) to the left and the root stele to the right. Section is 15 µm thick. Bright field. X30.

B. Light micrograph indicating starch distribution in parenchymatous tissue in leafy spurge. Starch (St) is uniformly distributed within the cells in an area between the vasculature (V). Section is 15 µm thick. Bright field. X192.


RS
V
V
A
VM
VM
B
VM

extension of the vascular strands. The vessel members are fewer in number and have a larger diameter than the more numerous tracheids on either side. Some parenchyma cells associated with the tracheary elements are also visible. Phloem is very poorly developed. As in Canada thistle, adventitious shoots differentiate centrifugally from the pericycle in the protoxylem region of the root. The vessel members at the site of the transition zone are more compressed than those in the shoot. The point of union of root and shoot resembles essentially an "elbow" joint.

Both in the roots and in the basal part of the adventitious shoot of leafy spurge, the cells are filled with starch grains that appear as PAS (Periodic acid Schiff's) - positive masses. Dense aggregations of starch grains in the pith cells of the shoot base extend into the root-stele beyond the transition area, and into the parenchymatous tissue of the root medullary ray (Fig. 12 A & B). Starch (St) is abundant in the parenchyma cells in the area between the two vascular strands but it is also found on the outer edge of both strands of vasculature (Fig. 12B). These aggregates of starch are not confined to any one region of the cell. The starch distribution within the parenchyma cells is somewhat irregular. Some cells contain starch confined to one end of the cell, indicating polarity, and others have a more uniform distribution (Fig. 12B). In general, starch distribution is denser in specimens where the root has undergone considerable secondary growth. No differences were observed in the degree of PAS staining. In addition, no differences in abundance of starch were found between cells in the distal and proximal areas of the shoot base or in the cells of the medullary ray.

Considering the first data on the root-shoot junction of both

FIGURE 11. A. Light micrograph of the median longitudinal section of leafy spurge shoot present on the root. Two strands of vasculature (V) separate the tracheary elements of the root stele (RS) to the left, and the shoot to the right. Section is 12 µm thick. Bright field. X40.

B. Light micrograph of the transition zone between the root and the shoot in leafy spurge. Individual vessel members (VM) are seen in transection (on the left) in the root and in a longitudinal plane (on the right) in the shoot. Section is 12 µm thick. Bright field. X256.

S
V
V
RS
A
V
V
B

Canada thistle and leafy spurge obtained from sectioned material, examination of cleared whole mounts added another dimension to the reconstruction of the vascular anatomy. The area of the vascular link between the root and shoot of Canada thistle forms only a small portion of the total width of the stem (Fig. 13A). Although the median trace was shown to consist of two bands (Fig. 8A & B, page 66) of vascular strands, the clearing (Fig. 13A) reveals that numerous collateral bundles are present in the shoot diverge a short distance from the point of union with the root. Even though there are two main conducting strands leading from the root stele, the shoot, nevertheless, has a single ring of collateral bundles, usually 7 to 9, and containing patches of parenchyma cells in its basal regions.

Less success was realized with leafy spurge in the clearing of whole mount tissues. Vascular bundles (VB) connecting the oot and the shoot can be seen, nevertheless, as darkened strands against a lightened area of surrounding cells (Fig. 13B). As in Canada thistle, the conducting tissue at the base of the shoot is arranged in a single ring of small vascular bundles, but in contrast to Canada thistle, there is little separation by parenchyma cell rays. The central core of the shoot consists of densely packed cells that have been shown to be starch-bearing (Fig. 12B). In the root of leafy spurge there is considerable secondary growth, mostly thick tracheids and a few vessel members. The result is a solid core of woody tissue, circular in outline, bordered by a cortex which has several starch-bearing cells. Small darkened areas in the cleared tissue are attributed to resistant plant constituents and resins which were not removed by the clearing agent.

FIGURE 13. A & B. Light micrograph of a portion of Canada thistle root (A) and leafy spurge root (B) with an adventitious shoot that was cleared with sodium hydroxide, and that shows the vascular link between the shoot (S) and root (R). Vascular bundles (VB) are prominent in the shoot. Transmitted light. X30.

VB
A
VB
B

DISCUSSION

Young Canada thistle plants exhibit more rapid translocation of ^{14}C-assimilates than leafy spurge plants, although the distribution of ^{14}C over time is the same. The pattern of distribution of assimilates throughout all the experiments is consistent. In treated plants most of the $^{14}CO_2$ fixed is retained as ^{14}C in the treated shoot. For the ^{14}C exported, the major sink is the root system. This agrees with previous reports on perennial dicots (7, 20, 23) and grasses (9, 17, 19, 39, 40, 41, 63). It is impossible to compare directly the amount of exported ^{14}C from treated shoots of herbaceous dicots with that in grass species because of the nature of the plants involved but the present findings are of the same order as those reported for couchgrass (17) and Italian ryegrass (40). During early growth, labelled assimilates accumulate in grasses in the most actively growing regions of the treated shoot and to a limited extent in the root apices (17, 32, 63). Translocation of assimilates to the roots takes place in dicots when plants are very young, provided that actively growing adventitious roots are present (20, 30, 31). With increasing size and age of plants, the roots constantly import more ^{14}C (20). The growth stage of Canada thistle and leafy spurge influences the translocation of ^{14}C to the roots, contrary to an earlier report (23) involving the same species. Greater export of ^{14}C to the roots is attributed either to an increased export potential within the shoot and/or the activity of a rapidly expanding root system with its numerous root apices. In grasses, reciprocal exchange of radiocarbon between a tiller and main shoot occurs principally via a direct pathway through

stem tissue rather than via a pathway involving roots (9). This is not the case in Canada thistle.

Certain leaves of Canada thistle are more important than others in assimilating $^{14}CO_2$ and subsequently exporting the ^{14}C-assimilates. Although the leaf area is not considered to be a major factor in $^{14}CO_2$ assimilation, the position the leaf occupies on a stem does influence its capability to export ^{14}C-assimilates to the root. The upper half and the lower half of a plant do not differ in their ability to export ^{14}C-assimilates to the roots. Reports on other species (37, 63) suggest that the lower leaves tend to supply the roots with assimilates. More ^{14}C-assimilates are translocated to Canada thistle roots following treatment of whole shoots. Similar observations are reported for grasses (Italian rye grass) in which whole tillers and individual laminae on tillers were exposed in the same way (40).

Translocation of ^{14}C-assimilates from a primary shoot to a secondary shoot is minimal. Secondary shoots of the plants under study are considered self-supporting (29) and, therefore, theoretically should be independent of assimilates from the primary shoot. At least trace amounts of ^{14}C were detected in all secondary shoots present, unlike previous work on the same species (23) which indicated that some but not all shoots other than the one fed accumulated ^{14}C-assimilates. The presence of ^{14}C was detected principally in the apices but it was distributed throughout the entire root system. The roots accumulate more of the ^{14}C exported than any of the secondary shoots and the presence or absence of secondary shoots did not alter the preferential accumulation of ^{14}C in the roots regardless of the growth stage examined.

The occurrence of comparatively more ^{14}C in the roots and secondary shoots at 10°C than at higher temperatures suggests that the translocation out of a treated shoot was highly sensitive to temperature. Reports on other species indicate that optimum translocation occurs between 20 and 30°C (37). The discrepancy can be explained in part by the short period of temperature adaptation before the exposure to $^{14}CO_2$.

In Canada thistle, there is a mutual exchange of metabolites between a primary shoot and secondary shoot along the same root piece. However, as each of the shoots continues to grow, the amount of metabolite transferred between the adjacent shoots does not increase and the difference between the amount of assimilate recovered from the roots of plants in either situation is not significant. The reciprocal exchange between shoots of approximately equal size poses a number of problems which cannot be explained in terms of the simplest hypotheses of source-sink relationships. That an adjacent shoot of about the same growth stage as a treated shoot imports ^{14}C-assimilates is remarkable (29). The existence of a reciprocal exchange between the two shoots means that each must simultaneously be both a source and a sink. Although the root acts as an intermediary in this instance for the transport of assimilates between the shoots, it is more probable that its role is that of a highly competitive sink. Younger shoots are not favoured in the reciprocal exchange at the expense of older shoots when more than one secondary shoot is present. There is no real evidence for competition for assimilates among secondary shoots. When the end shoot is treated, the sister shoots receive a greater proportion of the exported ^{14}C than the primary shoot. This preferential support

of the sister shoot may be a consequence of an easier vascular pathway between such shoots than the one which links the end shoot and the primary shoot. The fact that some label was recovered from the primary shoot 30 cm from the treated end shoot demonstrates the integrated nature of the plant system. The primary shoot is not only a key source of assimilates but behaves as a sink as well. The reason why it would be a sink is that the primary shoot continues to require assimilates for such functions as formation of new propagules (adventitious shoots and root buds). The closer the sink (secondary shoot or root bud) is to the treated shoot, the greater advantage it has in the accumulation of assimilates. The distance that a secondary shoot (or even a primary shoot) can be from a treated shoot and still receive ^{14}C-assimilates remains conjectural.

The vascular connection between a shoot and its parent root for both Canada thistle and leafy spurge is similar. The prominent feature which is significant with respect to the junction is the uninterrupted extension of two collateral bundles from the protoxylem poles of the root to the shoot. To my knowledge, there are no reports in the literature on the vasculature of shoots present on the roots of perennial weed species. The vasculature of the root-shoot junction corresponds with observations on the vasculature of shoots present on a hypocotyl (50). There is no evidence of an anatomical block that prevents the translocation of assimilates, in serial sections and whole mount studies. It is entirely possible that metabolism in the meristematic region of the shoot may be so rapid that photosynthates moving towards the apex of an individual shoot are completely consumed in the region of the junction and that any tracer (^{14}C) moving in the

assimilate flow accumulates there. Although the translocation pathway is not completely interrupted, the junction must nevertheless constitute a major bottleneck for the movement of assimilates in and out of the shoot. When the shoot is very small, it doubtless receives most of its assimilates from the root. Since the procambial area (Figure 10B) in the very early stages has no protophloem, carbohydrates must move in the cytoplasm from cell to cell. There is evidence in leafy spurge plants that hypocotylary buds initially show some growth independent of vascular connection (50); mobilization of carbohydrates occurs by simple diffusion without the mediation of vasculature. This line of evidence strongly supports the hypothesis that this same process is probably important in the area where the procambium separates the vasculature of root and shoot. The area contains no functional phloem elements. By diverting assimilates to the cytoplasm of actively growing procambial cells, the constriction would tend to maintain a high level of assimilates in these cells. The well developed vascular system observed in the center of the shoot makes it possible for some photosynthates to travel from the root to a shoot (presumably to the distal growing region of the shoot). It is suggested, therefore, that the restriction on the translocation of assimilates is to a large extent metabolic rather than anatomical and the restriction serves to divert ^{14}C-assimilates to the meristematic sinks.

Assuming that foliarly applied phloem-mobile herbicides move together with assimilates (53), the information gained from the translocation of ^{14}C-assimilates is useful in predicting the behavior of such herbicides within the plant. It is suspected that a herbicide would move to the roots more rapidly in Canada thistle than in leafy

spurge plants. The interception of spray and greater absorption by the leaves of Canada thistle have been suggested as the reasons for differences in susceptibility to glyphosate by both species (24). However, the rate of movement of the herbicide may further influence its effectiveness.

Although phloem-mobile herbicides are able to move to portions of the roots, the present study indicates that the largest portion of the ^{14}C-assimilates remains in the treated shoot. Maximum spray coverage and retention by the shoot, particularly the middle leaves, should allow maximum accumulation of herbicides (moving with assimilates) in the roots to take place. Accumulation of such herbicides in the roots should take place to a greater extent at reduced temperatures. The more herbicide going to the root, the better the chance for complete kill. If small secondary shoots are sprayed with herbicides then not only do the roots receive the chemical but the primary shoot at some distance from such shoots also receives some of the herbicide. If sufficient herbicide accumulates in the primary shoot then the potential for continued vegetative propagation is reduced.

The results of the present study indicate that the largest portion of ^{14}C-assimilates not retained in the shoot was found in the root. In addition, roots are much greater sinks for ^{14}C-assimilates than secondary shoots. If phloem-mobile herbicides behave in a similar manner to assimilates then they exercise their lethal effect by accumulation in the roots and not the secondary shoots.

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